Transfer of Leaf Rust Resistance Genes from Wild Species to Common Wheat

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I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in a part been submitted at any university for a degree.

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Summary

A wild species collection that consists of 928 accessions which represent 27 species of the genus *Triticum* (877 accessions) and 12 species of the genus *Thinopyrym* (51 accessions) was screened for resistance to leaf rust. The initial screening was done with an inoculum mix of the 5 pathotypes UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13. A total of 231 accessions (222 from the genus *Triticum* and 9 from *Thinopyrum*) proved to be resistant/moderately resistant to all races. An attempt was made to determine the following with regard to each resistant accession: (i) Can it be crossed successfully with common or tetraploid wheat? (ii) Is the resistance expressed sufficiently in the presence of the wheat genomes? (iii) Is it possible to transfer the resistance into wheat genomes? Seventy nine accessions have not yet been crossed successfully while the remaining 143 (representing 20 species) were crossed with common wheat or tetraploid wheat, depending on the ploidy level of the wild parent. The interspecific hybrids mostly had distinct phenotypes or were validated by doing root tip chromosome counts. A number of transfer attempts failed in the F_1 as a result of one of the following: Suppression or irregular expression of the resistance (60 accessions of *T. monococcum*, *T. turgidum*, *T. timopheevii*, *T. syriacum*, *T. triunciale*, *T. triaristatum*, *T. ovatum*, *T. sharonense*, *T. searsii*, *T. longissimum*, *T. crassum*, *T. cylindricum* and *T. dichasians*), the formation of embryoless seeds or poor F_1 viability (7 accessions). In 76 hybrids the resistance is fully expressed and these are now in a various stages of backcrossing to wheat. In some instances the chromosome number of the hybrids had to be doubled beforehand to ensure fertility during backcrossing. Thus far, the hybridization programme succeeded in producing: hybrid F_1's with 21 accessions, B_1F_1's with 13 accessions, B_2F_1's with 16 accessions, B_3F_1's with 13 accessions, B_4F_1's with 6 accessions and B_5F_1's with 2 accessions. The most advanced generations (B_3F_1, B_4F_1 and B_5F_1) represent the following 11 *Triticum* species: *T. turgidum* (AABB), *T. timopheevii* (AAGG), *T. speltoides* (SS), *T. sharonense* (SS), *T. kotschii* (UUSS), *T. peregrinum* (UUSS), *T. columnaris* (UUMM), *T. macrochaetum* (UUMM), *T. ovatum* (UUMM) and *T. triaristatum* 4x (UUMM). A hexaploid or near hexaploid wheat background has been restored in 17 cross combinations. The species sources of the 76 successful combinations were retested with the individual leaf rust pathotypes. In view of the abundant resistance detected among the *Triticum* accessions, it was decided not to attempt crosses with the resistant *Thinopyrum* accessions at this stage.

Opsomming

'n Wilde-spesie versameling bestaande uit 928 aanwinste, wat 27 spesies van die genus *Triticum* (877 aanwinste) en 12 spesies van die genus *Thinopyrum* insluit (51 aanwinste), is getoets vir blaarroesweerstand. Die aanvanklike sifting is gedoen met 'n inokulum-mengsel van 5 blaarroes-patotipes, te wete, UVPrt2, UVPrt3, UVPrt8, UVPrt9 en UVPrt13. 'n Totaal van 231 aanwinste (232 uit die genus *Triticum* en 9 uit die genus *Thinopyrum*) is gevind om matig bestand tot bestand te wees teen al die rasse. 'n Poging is aangewend om die volgende vas te stel met betrekking tot al die bestande aanwinste: (i) Kan dit suksesvol verbaster word met gewone of tetraploïede koring? (ii) Word die weerstand in die basters voldoende uitgedruk in die teenwoordigheid van die koringgenome? (iii) Sal dit moontlik wees om die weerstand oor te dra na koringchromosome? Nege-en-sewentig aanwinste kon tot dusver nog nie suksesvol met koring gekruis word nie terwyl die oorblywende 143 (verteenwoordigend van 20 spesies) wel gekruis is met gewone of tetraploïede koring, afhangende van die ploïedievlak van die skenkerouer. Die interspesie-basters het meesal duidelik uitkenbare fenotipes ge-openbaar of kon bevestig word by wyse van wortelpunt-chromosoomtellings. 'n Aantal verbasteringspogings het in die F_1 gefaal vanweë een van die volgende redes: Onderdrukking of ongereelde uitdrukking van die weerstand (60 aanwinste van *T. monococcum*, *T. turgidum*, *T. timopheevii*, *T. syriacum*, *T. triunciale*, *T. triaristatum*, *T. ovatum*, *T. sharonense*, *T. searsii*, *T. longissimum*, *T. crassum*, *T. cylindricum* en *T.dichasians*), die vorming van embrio-lose sade of lae lewenskragtigheid van die F_1 (7 aanwinste). In 76 basters is die weerstand volledig uitgedruk en hierdie materiaal verkeer tans in verskillende stadia van terugkruising na koring. In sommige gevalle moes die chromosoomgetalle van die basters vooraf verdubbel word ten einde vrugbaarheid tydens terugkruising te verseker. Tot dusvêr kon die verbasteringsprogram die volgende daarstel: Baster F_1's vanaf 21 aanwinste, T_1F_1's vanaf 13 aanwinste, T_2F_1's vanaf 16 aanwinste, T_3F_1's vanaf 15 aanwinste, T_4F_1's vanaf 6 aanwinste en T_5F_1's vanaf 2 aanwinste. Die mees gevorderde generasies (T_3F_1, T_4F_1 en T_5F_1) verteenwoordig die volgende 11 *Triticum* spesies: *T. turgidum* (AABB), *T. timopheevii* (AAGG), *T. speltoides* (SS), *T. sharonense* (SS), *T. kotschii* (UUSS), *T. peregrinum* (UUSS), *T. columnaris* (UUMM), *T. macrochaetum* (UUMM), *T. ovatum* (UUMM) en *T. triaristatum* 4x (UUMM). 'n Heksaploïede of naby-heksaploïede koring-agtergrond is reeds herstel in 17 kruisingskombinasies. Die weerstand in die spesiesbronne is ook gekontroleer deur elkeen te hertoets met die indiwidu.le blaarroespatotipes. Vanweë die rykdom van weerstandsgene wat onder die *Triticum* aanwinste gevind is, is daar besluit om voorlopig nie die bestande *Thinopyrum*-aanwinste te benut nie.

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1. LITERATURE REVIEW

1.1. Introduction

> "The great achievement of the modern agriculture is in its ability to produce consistently high yields across years and over a large land surface. This results from the minimization and alleviation of yield-depressing stresses such as inadequate soil fertility, water deficits, biotic pests, as well as the genetic adaptation of crops to a range of diseases and diverse climates" (Amir & Sinclair, 1994).

Roughly 10 000 years ago human populations in the Fertile Crescent must have shown a certain preference for the wild wheats (Porceddu et al., 1988). At the time when they faced difficulties with their food supply and conceived the idea of growing plants, Triticums were among the plants selected for cultivation. Apparently, from the very beginning preference was given to certain ear characteristics such as a non-brittle rachis and ready threshability. This established the onset of a selection pressure, either naturally or unconsciously guided by man.

Generation after generation agriculture spread in different parts of the old world exposing plant populations to different environments, thus widening the gate for gene mutation and introgression (Porceddu et al., 1988). This enriched the crops with new genes that recombination rearranged in the genome and exposed to selective pressure. In this way a wealth of forms, grouped in environmentally buffered complexes, were created on which agriculture had to rely until the last century.

Since the beginning of the last century man increased the selection pressures, which initiated a slow but constant process of genetic erosion. During the last forty years this erosion spread all over the world concomitantly with the production of new improved varieties. Genetically uniform varieties are being cultivated over large areas. Such varieties mostly carry single genes for resistance to biotic stresses and possess the potential to transform simple disease or pest attacks into epidemics (Porceddu et al., 1988; Feldman, 1988). The new varieties have high harvest indexes, lack vegetative aggressiveness and therefore perform unsatisfactorily under stress conditions. They require high cultivation inputs and appropriate agronomic management, while their yields almost reached a maximum due to the limit on the amount of dry matter that can be diverted into the grain (Porceddu et al., 1988).

Breeding and large scale monoculture of a crop impoverish its genetic base. It is therefore imperative that existing gene pools be conserved while new gene sources are identified and utilized in breeding programmes (Gill et al., 1985). The development and worldwide spread of improved wheat cultivars seem to have almost fully exploited and decimated the genetic resources of primitive cultivars and old landraces (Feldman & Sears, 1981; Knott & Dvorák, 1976; Feldman, 1988). Utilization of pest resistance genes from other cultivated cereals such as rye and barley for wheat improvement may be self-defeating because it potentially increases the overall genetic vulnerability of the three cereal crops (Gill et al., 1983). What remains then as a major source of genetic variation for wheat improvement are the wild species which hold vast potential for broadening the genetic base of cultivated wheat (Feldman & Sears, 1981; Gill et al., 1983, 1985; Feldman, 1988). The incorporation of this potential through induced homoeologous

recombination may yield genotypes with new desirable alleles and at the same time allow intergenomic repatterning for more favourable gene combinations (Kushnir & Halloran, 1984).

1.2. Genetic resources, preservation now - security in the future

Concern has been expressed worldwide regarding the danger of narrowing the genetic base and the genetic vulnerability of cereal crops (Gill et al., 1983; Feldman & Sears, 1981; Sears, 1981; Feldman, 1988). If the loss of plant genetic resources continues unabated at the present rate, genetic options for necessary changes in agricultural production in the future will be lost for ever (Jiang et al., 1994). The plant genetic resources provide the basic raw materials for adapting crops to, respectively, the expanding biotic and abiotic stresses, changing consumer preferences, possible changes in the environment (as may occur through global warming), rising sea levels and the depletion of the ozone layer. Crops will have to be adapted to sustainable forms of agriculture while maintaining increased productivity to feed the ever growing world population. In this context attempts are being made to preserve land races and wild species whose habitat is constantly declining (Porceddu et al., 1988; Rajaram et al., 1993; Hawkes, 1977; Harlan, 1976; Jiang et al., 1994).

Conservation, as an only option, is a prerequisite for the future utilization of the largely untapped genetic resources of wild species. The natural populations harbour rich genetic diversity which is ecogeographically structured and largely adaptive, locally, regionally and globally (Nevo, 1988; Feldman & Sears, 1981).

1.3. Systematics of cultivated wheats and their wild relatives

1.3.1. Classification

It has been shown by Sakamura (1918 in Knott, 1989a) that the wheats fall into three groups (ploidy levels) with chromosome numbers of 14, 28 and 42, where seven is the basic chromosome number. Thus, the chromosomes of each genome of the Triticinae fall into seven distinct homoeologous groups, where each genome accommodates one chromosome pair of each homoeologous group (Feldman & Sears, 1981).

In early classifications the wheats and their relatives (genera *Triticum* L. and *Aegilops* L.) along with the genera *Secale* L., *Agropyron* Gaertn., and *Haynaldia* Schur. formed a subtribe, the Triticinae, within the tribe Triticeae Dumont. (Morris & Sears, 1967).

Initially those species (most of them cultivated) that have an A-genome were the only species included in the genus *Triticum*. Within the three ploidy levels species were distinguished largely on the basis of morphological characters (Table 1) (Knott, 1989a). Revisions in the nomenclature of the Triticinae were made after the discovery that two of the hexaploid wheat (*Triticum aestivum*) genomes come from diploid *Aegilops* species. The early classification of species within the two genera *Triticum* and *Aegilops* as proposed by Mac Key (1966, 1968) is presented here in Table 2. Presently, many taxonomists, hence not all, include the species formerly belonging to *Aegilops* in *Triticum*. Another major change was the consolidation of former *Triticum* species

with the same genome formula and ploidy level into single species (Knott, 1989a). These adaptations are reflected in the classification proposed by Kimber & Sears (1987) (Table 2).

Early classifications of the perennial Triticeae used to include well over 100 of the perennial grass species with one spikelet per node in the genus *Agropyron* (Pienaar, 1990). Hybridization experiments, genomic analyses and cytogenetic investigations brought to light the need for a new classification system that would reflect more accurately the phylogeny and biological relationships of these taxa.

The genomic system of classification of the perennial Triticeae that recognizes 13 genera (*Agropyron*, *Australopyrum*, *Elymus*, *Elytriga*, *Festucopsis*, *Hordelymus*, *Hordeum*, *Leymus*, *Pascopyrum*, *Psathyrostachys*, *Pseudoroegneria*, *Secale* and *Thinopyrum*) with defined genomes or genome combinations were therefore developed. (Dewey, 1984; Mujeeb-Kazi & Wang, 1995).

Among the perennials the genus *Thinopyrum* is the most closely related to wheat (Mujeeb-Kazi & Wang, 1995). *Thinopyrum* contains three species complexes which comprise approximately 20 species (Dewey, 1984 in Pienaar, 1990). Each complex has sectional status.

The section Thinopyrum (*Junceum*) includes the species of the *Thinopyrum junceum* complex, e.g. *Th. runemarkii* ($8x$ = JbJbJbJbJbJbJb), *Th. junceum* ($6x$ = JbJbJbJbJeJe), *Th. distichum*, *Th. junceiforme*, *Th. satorii* ($4x$ = JbJbJeJe), *Th. bessarabicum* ($2x$ = JbJb) (Dewey, 1984; Pienaar, 1990; Mujeeb-Kazi & Wang, 1995).

The section Lophopyrum (*Elongatum*) is composed of the species of the *Thinopyrum elongatum* complex. The complex includes: *Th. ponticum* ($10x$ = JbJbJbJbJeJeJeJeJeJe), *Th. turcicum* ($8x$ = JbJbJbJbJeJeJeJe), *Th. curvifolium* ($4x$ = JbJbJbJb), *Th. scirpeum* ($4x$ = JeJeJeJe), *Th. elongatum* ($2x$ = JeJe), etc. (Dewey, 1984; Mujeeb-Kazi & Wang, 1995; Pienaar, 1990).

The third section, Trichophorae (*Intermedium*) consists of the species of *Thinopyrum intermedium* complex, e.g. *Th. intermedium*, *Th. gentryi* ($6x$ = JbJbJeJeJSJS), *Th. caespitosum*, *Th. nodosum* ($4x$ = JeJeSS) (Dewey, 1984; Mujeeb-Kazi & Wang, 1995; Pienaar, 1990).

1.3.2. Genome designation

An insight into genomic relationships among species can be gained by a study of chromosome pairing in their hybrids. This so-called "analyzer method", first employed by Kihara (Lilienfeld, 1951), has serious limitations yet has been of great value in taxonomic studies.

The analyzer method entails crosses with diploid "analyzer" species followed by a study of meiosis in the F_1. If the genome of the diploid analyzer shares homology with a genome of the species being tested, approximately seven bivalents should form with metaphase I (since 7 is the basic chromosome number in Triticeae). All hybrids involving nondonor diploid "analyzers" should, at meiotic metafase I, have 21 or more univalents. The result of the application of this method was the assignment of genome designations to the annual Triticinae (Table 2). Since Kihara's work a number of cytogenetic studies have resulted in changes to the genome designations made using the analyzer method.

The use of two classification systems, one treating *Aegilops* and *Triticum* as separate genera and the one combining them into a single genus, has led to considerable confusion over the years.

The multitude of names not only represents the diverse views of taxonomists, but also the diversity of the species themselves. To reduce the confusion, Kimber & Feldman (1987b) have compiled a synonym list of the most commonly used names among the *Triticum/Aegilops* groups (Table 3).

In this discussion the classification system as proposed by Morris & Sears (1967) and modified by Kimber & Feldman (1987b) will be used throughout.

1.4. Evolution of *Triticum*

Evolution in the Triticeae is a complex anastomosis of general processes and singular events (Kimber & Feldman, 1987a) which traces back in origin to the evolution of angiosperms some 130 million years ago (Porceddu et al., 1988). During that period, *Triticum* species, presumably descended from a common ancestor, had diverged into a number of diploids. Diversification continued with their spread in different climatic and ecogeographical areas. Dvorák & Zhang (1992) derived a phylogenetic tree depicting a probable pattern of diversification of some of these diploid species (Fig. 1). Convergence in various and subsequently modified combinations resulted in the formation of polyploids (Fig. 2, 3 & 4) (Kimber & Feldman, 1987a; Porceddu et al., 1988). Being both the centre of origin and the main centre of diversity for the genus *Triticum*, the Fertile Crescent is a region with a rich concentration of *Triticum* species, both diploids and polyploids, each exhibiting a considerable range of ecological and morphological variation (Feldman & Sears, 1981). The mixed populations in which these species often grow facilitate spontaneous hybridization and thus interspecific and intraspecific gene flow (Kimber & Feldman, 1987a; Feldman & Sears, 1981; Yamashita & Tanaka, 1968). These evolutionary events built up a wealth of genetic variation thus making the region an active centre of evolution (Feldman & Sears, 1981).

1.5. Pivotal-differential hypothesis

It was pointed out by Zohary & Feldman (1962) that the polyploid species, morphologically and cytogenetically, fall into three natural groups: one sharing the A-genome of *T. monococcum*, one sharing the D-genome of *T. tauschii* and one sharing the U genome of *T. umbellulatum*. Following an extensive investigation of the U-genome group of species and the occurrence of natural hybridization among them, Zohary & Feldman (1962) suggested the "pivotal-differential" hypothesis for the evolution of the three genome clusters A, D, and U. This hypothesis states that within each cluster, species are characterized by an unaltered pivotal genome in addition to a varied number of modified genomes that were designated as being differential. Apparently the common genome in each group remained relatively unaltered by hybridization, thus acting as a buffer of stability around which chromosome substitutions and recombinations took place within the unshared genomes. These so-called pivotal genomes therefore facilitated introgression and inter-amphidiploid gene-flow (Kimber & Feldman, 1987a; Zohary & Feldman, 1962) by allowing for the survival and perpetuation of the polyploid while recombination and stabilization of the modified genome(s) took place. As a result of genome differentiation each natural group of

present-day polyploid species exhibits almost continuous variation for numerous characters (Kimber & Feldman, 1987a). Polyploidization was therefore of great evolutionary significance as it facilitated the genome rearrangements that are largely responsible for the wide variation among polyploid *Triticum* species (Zohary & Feldman, 1962).

1.5.1. U-genome cluster

The clearest demonstration of the pivotal-differential hypothesis is provided by the U-genome cluster (Fig. 2). In this cluster the U-genome acted as the pivotal genome that imparted relative stability in the polyploids and allowed for subsequent alteration of the accompanying genome(s) following inter-species hybridization (Kimber & Feldman, 1987a). Evidence was found of the occurrence of hybridization of present-day U-genome tetraploids in shared populations and of apparent introgression of characters between them (Zohary & Feldman, 1962). Introgression also took place to and from diploids that occurred sympatrically with the mixed tetraploid populations (Kimber & Feldman, 1987a).

1.5.2. D-genome cluster

The pivotal role of the D-genome in the D-genome cluster is not as clear, due to the modification of the genome in some species. This cluster may be subdivided into three groups (Kimber & Zhao, 1983; Zhao & Kimber, 1984). The first group, including *T. cylindricum*, *T. ventricosum* and *T. aestivum*, exhibits no or little modification of the *T. tauschii* D-genome. The second consists of the tetraploid and hexaploid forms of *T. crassum* which have somewhat modified D-genomes. The two D-genomes present in the hexaploid *T.crassum* (6x) pair preferentially with each other to the exclusion of the D-genome of *T. tauschii* (Kimber & Feldman, 1987c). The third group including *T. juvenale* and *T. syriacum* has undergone substantial modification of the D-genome. Nevertheless, this group of species clearly exhibits features inherited from *T. tauschii* (Fig. 3) such as, barrel-shaped spikelets and disarticulation of the spike at maturity. (Kimber & Feldman, 1987a).

1.5.3. A-genome cluster

The A-genome cluster includes all the commercially important cultivated wheats (Fig. 4). Excepting *T. tauschii*, all the species have the A-genome and it can be suspected that similarity for this genome is essential. Based on the degree of meiotic pairing between the A-genome chromosomes of the diploid wheats and the A-genome telocentrics of *T. aestivum*, Kimber & Hulse (1978) and Kimber et al. (1981) concluded that the A-genome chromosomes of *T. aestivum* are substantially unaltered from the A-genome chromosomes of the diploid wheats. The only exception was chromosome 4A which did not show homologous affinity to any of the diploid A-genome chromosomes (Miller et al., 1981). Moreover, a chromosome similar to 4A of *T. dicoccoides* was observed in *T. araraticum* and *T. speltoides* only. Analyses of the pairing of *T. aestivum* 4A telosomes with chromosome 4A of *T. araraticum* and 4S of *T. speltoides* further confirmed this (Chen & Gill, 1983). However, chromosome 4A of common wheat has since been

reallocated to the B-genome as chromosome 4B, while the previous chromosome 4B is now regarded as being the real chromosome 4A (Morris, 1988).

Kimber & Feldman (1987a) regarded the B-genome as being a possible differential genome in the A-genome cluster, since it has not been unequivocally assigned to any particular diploid species. Furthermore, no diploid with genomes homologous to the G-genomes has been identified, neither have relationships between the B- and G-genomes been completely clarified. Based on the meiotic pairing between *T. aestivum* B-genome telocentrics and G-genome chromosomes (Salle & Kimber, 1978) it was estimated that the G-genome has 47% homology to the B-genome (Kimber et al,. 1981). Wild forms of species having B- or G-genomes grow together and in association with cultivated forms in the Fertile Crescent, with substantial opportunity for introgression. Thus, it is possible that substantial homology does not exist between the B- or G-genomes and that of any particular diploid species (Kimber & Feldman, 1987a).

The evolutionary relationships in diploid and polyploid wheat can be viewed as an anastomosis based on the three pivotal genomes (A, U and D). Modification of these and of their associated genomes following hybridization between related polyploids, and also the introgression of genetic material from their sympatric relatives (Table 4) has generated a vast gene pool.

While the pivotal-differential hypothesis is fairly well visualized and supported by results from a number of studies, Waines & Bernhart (1992) disagree with the concept of "modified genomes" in the tetraploid species which, they think, may not actually be modified. Their reasoning is that Kihara's genome formulae were established on a very narrow base of 1-3 accessions of each diploid analyzer species. Thus, "nothing approaching the total morphologic nor geographic variation was present in Kihara's species collection". As a possible explanation for the "modified genomes" Kihara himself observed that the appropriate diploids might not yet have been found. Thus, considerable uncertainty still exist regarding the validity of the pivotal-differential hypothesis.

1.6. Progenitors and origin of common wheat

1.6.1. The origin of the A-, B- and D- genomes

Polyploid evolution and the phylogeny of the polyploid wheats have been the subject of intense research and speculation during the past 77 years. Various experimental approaches have been employed to ascertain the diploid progenitors of these wheats. Consequently, various species of the genus *Triticum* (including the former *Aegilops* species) have been implicated as the donors of their component genomes (Kerby & Kuspira, 1987). The difficulty in solving the phylogenetic relationships in *Triticum* derives from evolutionary changes in the genomes of polyploid wheats since their formation. Such changes may have been induced by the hybridogenic origin of the species, introgression of genetic material from other species and/or accumulation of loci or genetic systems coding quantitative characters which involved no major genome alternations (Konarev, 1983).

Cytogenetic studies revealed that the polyploid cultivated species constitute two evolutionary lineages (Fig. 5). One comprises *T. timopheevii* (2*n* = 4*x* = 28, AAGG) and *T. zhukovskyi* (2*n* = 6*x* = 42, AAAAGG), the other emmer wheat, *T. turgidum* (2*n* = 4*x* = 28, AABB) and *T. aestivum* (2n = 6*x* = 42, AABBDD) (Dvorák et al, 1993). In the first lineage *T. zhukovskyi* has originated from alloploidy between *T. timopheevii* and einkorn wheat which contributed its second set of A-genome homologues (Upadhya & Swaminathan, 1963).

In the second lineage (*T. turgidum* and *T. aestivum*) it is well known that *T. aestivum* has originated from alloploidy between emmer wheat and goatgrass, *T. tauschii* (2*n* = 2*x* = 14, DD) (based on cytological and taxonomical criteria) (McFadden & Sears, 1946; Chen & Gill, 1983). Isozyme analyses confirm this hypothesis (Nishikawa, 1983; Jaaska, 1980, 1984; Nakai, 1981; Lagudah & Halloran, 1989). These studies provide further detail on the origin of the D-genome of *T. aestivum* by suggesting that *T. tauschii* ssp. *strangulata* rather than ssp. *tauschii* has been involved. Moreover, isozyme studies suggested that the hexaploid wheats probably originated in the southern Caspian Sea - Transcaucasus region where ssp. *strangulata* occurred.

Molecular studies on chloroplast and mitochondrial DNA of *Triticum* species, suggested that emmer wheat was the female parent of *T. aestivum*. The organelle genomes of *T. aestivum* and emmer wheats show identical or similar restriction fragment length polymorphism (RFLP) and sequence variation (Bowman et al., 1983; Tsunewaki & Ogihara 1983; Grauer et al., 1989).

Emmer wheat and *T. timopheevii*, being tetraploids, are also the products of alloploidy between diploid species (Lilienfeld, 1951) (Fig. 5). Early cytogenetic studies by Sax in 1922 and Kihara in 1924 etc. (as in Dvorák et al., 1993) led to the conclusion that the A-genomes of both tetraploid species were contributed by *T. monococcum* (2*n* = 2*x* = 14, AA). C-band studies of the somatic chromosome complements of *T. monococcum* and *T. aestivum* were done by Gill and Kimber in 1974, and showed that the *T. monococcum* chromosomes were very similar to the *T. aestivum* A-genome chromosomes (Kerby & Kuspira, 1987). In hybrids derived from crosses between *T. aestivum* ditelosomics and *T. urartu*, Dvorák (1976) found that the *T. urartu* chromosomes paired only with the A-genome chromosomes of *T. aestivum*. Following the studies of Johnson & Dhaliwal (1976) on the reproductive isolation of *T. boeoticum* (*T. monococcum* ssp. *boeoticum*) and *T. urartu*, it became apparent that what was known as einkorn wheat actually comprised two biological species, i.e. *T. monococcum* and *T. urartu*. This was also borne out by the sterility of their hybrids. Following immunological studies of the properties of seed storage proteins, Konarev et al. (1979; 1983) concluded that the A-genome of *T. turgidum* was contributed by *T. urartu* and that of *T. timopheevii* by *T. monococcum*. Nishikawa (1983) suggested on the basis of isozyme variation that the A-genome in both lineages was contributed by *T. urartu*. This was confirmed by Dvorák (1988) and Dvorák et al. (1993) following studies of variation in repeated nucleotide sequences. Takumi et al. (1993) did RFLP analyses of nuclear DNAs of diploid and polyploid wheats, and concluded that the A-genome of emmer and common wheats originated in *T. urartu*. Sequential N-banding and *in situ* hybridization analyses done by Juang & Gill (1994) also suggested that *T. urartu* is the donor of both the A- and A^t-genomes of the polyploid wheats. Furthermore, results were obtained showing

that the second A-genome of *T. zhukovskyi* was contributed by *T. monococcum* (Dvorák et al., 1993).

Although the grandfather of hexaploid wheat, which was also the A-genome donor of emmer wheat, has been determined, this is not the case with the donor(s) of the B-genome (the grandmother(s) of common wheat). The question of its origin is still surrounded by controversy, despite numerous studies using biochemical, cytological, geographical, meiotic pairing and morphological approaches (for review see Kerby & Kuspira, 1987).

It is most likely that the B-genome donor(s) was a member of the group of species that made up the section Sitopsis of the former genus *Aegilops* (Table 2). The following species were suggested as being probable B-genome donors: *T. speltoides* (2n = 2x = SS) (Jaaska, 1978, 1980, 1984; Chen & Gill, 1983; Bahrman et al., 1988; Nishikawa, 1983); *T. longissimum* (2n = 2x = S^lS^l); (Nishikawa, 1983; Jaaska, 1978; Feldman, 1978; Konarev, 1983); *T. searsii* (2n = 2x = S^sS^s) (Feldman, 1978; Konarev, 1983); *T. sharonense* (2n = 2x = S^lS^l) (Kushnir & Halloran, 1981); and *T. bicorne* (2n = 2x = S^bS^b) (Sears, 1956 in Kerby & Kuspira, 1987). The cytoplasm of the tetraploid wheats was also contributed by the B- and G-genome donors, and that of *T. timopheevii* is similar to the cytoplasm of *T. speltoides* (Ogihara & Tsunewaki, 1988). Following a study of variation in repeated nucleotide sequences, Dvorák & Zhang (1990) concluded that of the extant genomes, the *T. speltoides* genomes are the most closely related to both the B- and G-genomes of the tetraploid wheats. After screening Triticeae species for hydroxamic acid content (secondary metabolites in wheat conferring resistance against aphids), Niemeyer et al. (1992) also suggested *T. speltoides* as the most likely B-genome donor. According to Fernandez-Calvin & Orellana (1990), *T. speltoides* is the only species from the former Sitopsis section that can explain the variability for high molecular weight glutenin subunits encoded by the wheat B-genome, and thus is a possible B-genome donor. Ogihara et al. (1994) found that RFLP patterns of the common wheat B-genomes most closely resembled those of *T. speltoides*.

Although a lot of effort has gone into attempts to attach the label "B-genome donor" to a particular species from the former Sitopsis section or even to *T. urartu*, effort was not spared in achieving the opposite. Numerous studies provided evidence against all the proposed B-genome donor species (for review see Kerby & Kuspira, 1987) . The latest studies of Fernandez-Calvin & Orellana (1993, 1994) rejects *T. speltoides, T. sharonense* and *T. longissimum*, as putative donors of the B-genome of common wheat on the basis of meiotic pairing behaviour as analyzed by the C-banding technique.

Zhirov (1989) conducted a study on common wheat and former *Aegilops* species, hybrids between the most probable A- and B-genome donors, their synthetic tetraploids and hybrids of selected genome composition. On the basis of meiotic pairing results he concluded that the B-genome originates from chromosomal recombination between the A-genome and any S-genome from the former *Aegilops* section Sitopsis. Two pathways for the origin of polyploid wheat were suggested with the following believed to be the more likely: S egg cell + A male nucleus = AS diploid, AS unreduced egg cell + A male nucleus = AAS triploid, AAS unreduced egg cell + A

male nucleus = AAAS tetraploid. Zhirov & Ternovskaya (1993) provided further data in support of a chromosome recombination origin for the B-genome. They analyzed chromosome pairing in hybrids using the capacity of *T. speltoides* to suppress the wheat genetic system for control of homoeologous pairing. Zhirov & Ternovskaya (1993) also suggested that the tetraploid wheat *T. turgidum* is a segmental tetraploid.

Based on the observation that *T. dicoccoides* (genomes = AB) shows much larger RFLP variation at the nuclear DNA level than *T. timopheevii* ssp. *araraticum* (genomes = AG) it has been suggested by Mory (1991 in Miyashita & Tsunewaki 1993) that *T. dicoccoides* is older than *T. timopheevii* ssp. *araraticum*. The data give preference to a diphyletic (different combinations of parental species at different times) origins of emmer and timopheevii wheats, rather than a monophyletic origin (Miyashita et al., 1994). Results from RFLP analyses with wild tetraploid wheats (*T. dicoccoides* and *T. timopheevii* ssp. *araraticum*) done by Mori et al. (1995) support these findings and also favour a diphyletic origin for these species.

More results in favour of the diphyletic origin were obtained regarding the G-genome donor of the *T. timopheevii* (genomes = AG) - *T. zhukovskyi* (genomes = AAG) lineage. It was pointed out that *T. speltoides* has the best chance of being this donor, since the average number of bivalents formed per meiocyte in *T. timopheevii* x *T. speltoides* hybrids was 6.89 (Shands & Kimber, 1973). Variation in repeated nucleotide sequences and the structure of rRNA gene families supported the conclusion that the G-genome was derived from *T. speltoides* (Dvorák et al., 1989). Analyses of chloroplast DNA restriction site variation similarly supported *T. speltoides* var. *aucheri* as being the G-genome donor (Tsunewaki & Ogihara, 1983). Molecular variation in chloroplast DNA suggested that the plastotype (plastid genotype) of the *T. speltoides* accession studied was identical to the major plastotype of *T. timopheevii* ssp. *araraticum* (genomes = AG) (Miyashita et al., 1994).

1.6.2. Origin of common wheat, constraint on genetic variation

Presumably, during the evolution of tetraploid wheat only a small proportion of the genetic variation present in the diploid wheats was retained in the new tetraploids. The evolution of hexaploid wheat, that might have involved spontaneous crosses between tetraploid wheat and goatgrass, further narrowed this genetic base (Hatchett & Gill, 1981; Kushnir & Halloran, 1984). Subsequent diploidisation possibly provided another constraint on genetic variation in hexaploid wheat, since it might have imposed restrictions on intergenome gene exchange (Kushnir & Halloran, 1984). As a result, the wild species of the diploid and tetraploid ancestral forms constitute a relatively unutilized and accessible germplasm pool for broadening the genetic base of common wheat (Feldman & Sears, 1981).

1.7. *Triticum* species as genetic resource for plant adaptation

Over the years numerous studies by various workers revealed the value of the wild species as a potential source of genes for plant adaptation in the cultivated tetraploid and hexaploid wheats for

agronomic characters such as biotic and abiotic stress tolerance/resistance, protein content, leaf photosynthesis (Table 5).

1.7.1. Abiotic stress tolerance and seed protein content

Genetic improvement has played a dominant role in the evolution of wheat. Examples of this have been the modification of regulatory processes, such as altering the timing of the life cycle and the redistribution of assimilate (Evans, 1981).

Physiological or quantitative traits such as drought and salinity tolerance, cold hardiness, photosynthetic efficiency, protein content, are complex in inheritance and therefore relatively difficult to manipulate in a breeding program (Fedak, 1985). A number of investigations have revealed a wide range of variation for these characters among the wild species (Table 5).

1.7.1.1. Drought tolerance

Drought is the most important of all environmental constraints to wheat production in a number of regions of the world, particularly in Africa and West Asia. Short periods of drought during critical stages of crop growth can lead to substantial yield reductions. Moisture stress decreases protein synthesis, diminishes tissue hydration, induces rapid stomatal closure and therefore reduced transpiration and photosynthesis (Fedak, 1985).

Species that are noted as containing useful variation for xerophytic properties include *T. crassum* and *T. vavilovii* (Rifaie et al., 1981), *T. dicoccoides* (Blum et al, 1983), *T. longissimum*, *T. kotschyi* (the most xerophytic of the wild *Triticum* species), and *Agropyron junceum*, a slow growing perennial, adapted to sandy soils with low water-holding capacity (Shimshi et al., 1982). These species, although some of them are quite distantly related, can be crossed to wheat. However, due to the polygenic nature of the traits involved, and their normally low heritabilities gene transfer from these species is expected to be problematic.

1.7.1.2. Salinity tolerance

Salinity and related alkalinity are problems affecting wheat production in both arid and semi-arid regions. It is also an increasing problem in irrigated areas (Wright, 1993).

The growth of Triticums in saline soils is determined by their ability to limit the salt influx into the plant via the transpiration stream. It has been shown that this implies more than one physiological mechanism. Each such mechanism involves several steps and differ from species to species. In some species such as *T. tauschii*, salt tolerance is achieved through the ability to limit the accumulation of Na^+ and Cl^- and by maintaining high K^+/Na^+ ratios in the shoots (Gorham et al., 1990). The enhanced K^+/Na^+ discrimination character is present in most other D- and U-genome species (Gorham, 1990a) as well as in the A-genome of the diploid wheats *T. monococcum* ssp. *monococcum*, *T. boeoticum* and *T. monococcum* ssp. *urartu*. Expression of the A-genome mediated K^+/Na^+ discrimination ability is found in amphiploids derived from hybrids between tetraploid wheats (*T. durum*) and the A-genome diploid wheats. This suggests that the expression of the character must have been lost from the A-genome during the evolution of *T.*

durum (Gorham et al., 1991; Gorham, 1990b). Superior salt tolerance in the perennial wheat grasses appears to be associated with better control of salt accumulation, particularly at higher salt concentrations (>200 mol m^{-3} NaCl), rather than the enhanced K^+/Na^+ discrimination character which is found in the D-genome of wheat, and which functions at lower salinities (Gorham et al., 1986). This control of salt accumulation in the leaves permits osmotic adjustment to the external salinity, but thereafter prevents any further increase in the leaf salt load (McGuire & Dvorák, 1981; Gorham et al., 1986).

Salinity tolerance has been reported for: *T. tauschii* (Gorham et al, 1986; Shah et al., 1987; Gorham, 1990b; Wright, 1993), T. *sharonense* (Kimber & Feldman, 1987b), *T. boeoticum* (Kashour & Damania, 1991), and *T. dicoccoides* (Kashour & Damania, 1991; Nevo et al., 1993). The study of Nevo et al. (1993) identified genotypes of *T. dicoccoides* tolerating (spiking and ripening stages) concentrations up to 250 mM NaCl (equivalent to 40% sea water). These levels exceed the hitherto reported highest levels in semi-dwarf bread and durum wheat regarded as salt tolerant (Nevo et al., 1993).

A substantial level of salt tolerance was also found among species of wheatgrass, *Elitriga* Desv. (McGuire & Dvorák, 1981). Thirteen species (36 accessions) were compared with 6 wheat accessions, previously identified as salt tolerant. While no wheat accession survived a 250 mM NaCl concentration , several wheatgrasses survived even in 750 mM NaCl (A 50% higher concentration than the NaCl content of sea water). The four most tolerant wheatgrasses were: *E. scirpea*, *E. pontica*, *E. junceiformis* and *E. diae*.

1.7.1.3. Cold hardiness and frost tolerance

Frost resistance in wheat is thought to have developed during the Pleistocene epoch and to have arisen first in *T. boeoticum* (A^bA^b). This is probably the reason why *T. araraticum* (A^bA^bGG) showed the highest level of frost tolerance amongst wild tetraploids in a study done by Barashkova (1988).

T. tauschii has been regarded as a potentially valuable source of winter hardiness genes with high levels of frost tolerance (Le et al., 1986; Barashkova & Migushova, 1984). The tetraploid *T. cylindricum* (CCDD), also includes genotypes that are resistant to low temperatures (Barashkova & Migushova, 1984). With *T. cylindricum* having a cytoplasm similar to that of *T. tauschii* and also possessing the D-genome, Kimber & Feldman (1987b) suggested that its frost tolerance may be imparted by the D-genome. It is also believed that *T. tauschii* contributed to the frost resistance and ecological adaptability of the hexaploid wheats (Barashkova, 1988).

1.7.1.4. Leaf photosynthesis

Crop productivity and specifically grain yield of wheat, are genetically determined through a hierarchy of physiological processes with the central process being photosynthesis (Mahon, 1983). This is why the simultaneous improvement of both the photosynthetic efficiency and capacity of photosynthate utilization is receiving increased attention (Walker & Syvak, 1986; Carver & Nevo, 1990).

It is known that the cultivated wheats have lower photosynthetic rates, despite their having larger leaves, as compared to their ancestral forms (Evans & Dunstone, 1970). Austin et al. (1982) measured the photosynthetic rates in the flag leaves of 10 *Triticum* accessions (*T. monococcum, urartu, speltoides, tauschii, turgidum, dicoccoides,* and *dicoccum*) and 5 accessions of *T. aestivum*. Upon comparing the CO_2 fixation efficiencies with their ploidy levels, he concluded that the diploid and tetraploid species accessions equalled or exceeded the average photosynthetic rate (PR) of the 5 hexaploid wheats. The mean PR values ($mgCO_2\ dm^{-2}h^{-1}$) for diploid and tetraploid species and hexaploid wheat cultivars were respectively 38, 32 and 28. Genetic diversity for PR has also been found among 27 native populations (108 accessions) of *T. dicoccoides* (Carver & Nevo, 1990). Accessions having a high photosynthetic capacity of 38 and 32 $mgCO_2\ dm^{-2}h^{-1}$ (Austin et al., 1982) and 32.4 $\mu mol\ m^{-2}s^{-1}$ (the control averaging 24.3 $\mu mol\ m^{-2}s^{-1}$) (Carver & Nevo, 1990) constitute a potentially valuable genetic resource for the genetic improvement of hexaploid wheat.

The photosynthetic rates appear to be positively correlated with the numbers of stomata and veins per leaf, but negatively with leaf area, leaf width and mesophyll cells on the leaf (Austin et al., 1982; Carver & Nevo, 1990). The differences in photosynthetic rate may be due to different translocation efficiencies, allowing a better exploitation of solar energy (Dunstone et al., 1973) or different balances in sink size and leaf area (e.g. profuse tillering of diploid species, compared with polyploids, generate new sinks at the time of ear emergence and thus a requirement for prolonged and higher photosynthetic rates) (Fedak, 1985).

1.7.1.5. Protein content

Aaronsohn in 1913 was the first to realize the potential value of wild emmer (*T. turgidum* L. var. *dicoccoides*) for the improvement of cultivated wheats (Sharma et al., 1981). Accessions were found which possessed large grains and the potential for drought tolerance. Lawrence et al. (1958) found higher protein and lysine contents in the wild wheats (particularly in the genus *Agropyron* and the former genus *Aegilops*) as compared with bread and durum wheats.

Avivi (1978) determined the protein contents of 47 different collections of *T. dicoccoides*, representing the ecological range in Israel. The mean percentage in wild grown material was 23.3% (ranging from 17.0 to 27.3%), while the greenhouse grown, selfed wild material gave an average of 32.7% (ranging from 24.7 - 43.4%).

Sharma et al. (1981) explored variability for protein content in collections of the diploid and tetraploid progenitors of common wheat (*T. monococcum*, *T. turgidum* ssp. *dicoccoides* and *T. timopheevii* ssp. *araraticum*). The most promising accessions (from *araraticum* and *dicoccoides*) had 30.5% and 30.9% protein, respectively (the protein content of the Madoc durum check was 16.6%). Among the 93 *T. monococcum* accessions the highest protein content was 22.9%.

Numerous observations show an inverse correlation between grain protein concentration and yield in cereals (Bhatia & Robson, 1976). From the data (energy calculations) of Sinclair & de Wit (1975) it can be inferred that in any species, simultaneous increase in grain protein concentration and grain yield are incompatible. According to Harlan (1976) the observation that

cultivated cereals generally have lower protein contents compared to their wild progenitors is closely related to seed size. Selection for larger seeds resulted in reduced protein contents. In contrast Avivi (1978) reported no significant differences between the protein contents of seeds of different size and weight in a collection of *T. dicoccoides*. Moreover, a positive correlation between protein content and seed weight was found among *T. dicoccoides* collections grown in the wild. In general, the protein and lysine values of the diploids (Rafi et al., 1992) and tetraploids were found to be nearly twice as high as those of commercial wheat cultivars. In their study Madoc durum had a lysine content of 3.08% as compared to 7.53% for *T. dicoccoides*, 7.25% for *T. araraticum* and 6.10% for *T. monococcum*.

1.7.1.6. General

Damania & Altunji (1991) evaluated 662 *Aegilops* accessions from 24 species for tolerance to heat, frost and drought, as well as resistance to naturally occurring diseases and adaptability. Two hundred and six accessions (12 species) were resistant/tolerant, with *T. macrochaetum, columnare, ovatum* and *triunciale* being the most promising sources. In another study of 629 accessions from 26 species, the genotypes were tested for drought and frost tolerance. Ten species (153 accessions) were identified as being tolerant (Damania & Pecetti, 1990). An evaluation of more than 100 lines of *T. turgidum* ssp. *dicoccoides* (Damania et al., 1991) had shown them to vary for tolerance to frost and drought and resistance to rust infection. According to the report almost all the accessions had higher protein contents than the commercial wheat cultivars used as checks.

1.7.2. Tolerance/resistance to biotic stress

Pathogens and insects cause considerable crop losses and instability in wheat yield. Breeding for resistance had proved to be a cost effective control method. Due to the regular appearance of new races of pathogens and insects, different sources of resistance are constantly needed to compete with the continuously evolving virulence of the pest populations (Gill et al., 1985).

1.7.2.1. Resistance to pathogens

There is a wide range of genetic variation for disease resistance among the wild species of the genus *Triticum* (Knott, 1989b). Resistance to the cereal rusts is of particular interest as the rusts are still the most important diseases of wheat world wide (Schafer, 1987). The prime importance of rust diseases result from their wide distribution and long distance dissemination as well as their ability to mutate and attack previously resistant cultivars and cause severe losses under epidemic conditions (Schafer, 1987).

Decades of work revealed the potential of the wild species as a promising source of genes for resistance to pathogens and diseases. Evaluation of 969 *Triticum* accessions from 25 species showed that species with the S- (*T. speltoides*), C- (*T. dichasians*- previously *Ae. caudata*), U- (*T. umbellulatuma*) and M- (*T. comosum*) genomes often include a high proportion of resistant accessions (Dhaliwal et al., 1991). Gill et al. (1985) evaluated 187 *Triticum* (previously *Aegilops*)

accessions from 21 species for their reaction to *Puccinia recondita* and 37 accessions (16 species) for their reaction to powdery mildew (*Erysiphe graminis*). They found 124 accessions (16 species) to be resistant to leaf rust while 30 accessions (14 species) were resistant to powdery mildew. Valkoun et al. (1985) tested 487 *Triticum* (formerly *Aegilops*) accessions (21 species) and found seedling and adult plant resistance to: *P. graminis*, *P. recondita*, *P. striiformis* and *Erysiphe graminis*. Accessions of *T. speltoides*, *dichasians* (previously *Ae. caudata*), *sharonense* and *ovatum* (previously *Ae. geniculata*) often showed multiple resistance to all four diseases. Frauenstein & Hammer, (1985) found resistance to leaf rust and mildew in 16 *Triticum* (formerly *Aegilops*) species following the testing of 20 species (490 accessions). In another study of 282 *Triticum* (formerly *Aegilops*) accessions (19 species) 107 proved to be resistant to yellow rust and 240 resistant to powdery mildew (Singh et al., 1988). A test of more than a 1000 lines of 24 *Triticum* species (20 were former *Aegilops* species) for reaction to leaf rust, yellow rust, karnal bunt (*Tilletia indica*) and leaf spot disease (Dhaliwal et al., 1986) yielded a variety of resistance responses. The *T. monococcum* and *T. timopheevii* collections included accessions with resistance to leaf and yellow rust. Accessions with resistance to leaf rust, *T. indica* and leaf spot were also identified. Van Slageren & Mamluk (1991) evaluated 20 *Triticum* (formerly *Aegilops*) species (420 accessions) in a field test. One hundred and seventy seven accessions (44%) were resistant to yellow rust with an ACI value (average coefficient of infection) of up to 15MR for: *T. columnaris, comosum, speltoides, triaristatum* and *triunciale*. Damania et al. (1991) tested 266 *T. turgidum* ssp. *dicoccoides* lines for resistance to leaf rust, stem rust and yellow rust. The results showed resistance in 191 lines to yellow rust, in 253 to leaf rust and in 263 to stem rust.

Other reports of resistance among wild *Triticum* species included resistance to: leaf rust, yellow rust and mildew (Gill et al., 1987; Botchev et al., 1982; Zaharieva in Dimov et al., 1993); leaf rust (Gill et al., 1986; Damania & Skovmand, 1991), leaf and stem rust (Casulli et al., 1985), yellow rust (21 physiologic races) (Gerechter-Amitai & Stubbs, 1970; Mikhova, 1988; Damania & Pecetti, 1990; Damania & Skovmand, 1991), bunt (*Tilletia caries*) (Krivchenko et al., 1983), *Septoria tritici* (McKendry & Henke, 1994). Widespread leaf rust resistance has been reported in *T. speltoides* and *T. peregrinum* (previously *Ae. variabilis*) following the testing of 274 accessions belonging to 10 *Triticum* (formerly *Aegilops*) species (Manisterski et al., 1988).

The results of these investigations point at diversified indigenous populations of *Triticum* which possess genes conferring high levels of resistance to a wide spectrum of pathogens.

T. tauschii (formerly *Ae. squarrosa*), is of particular interest to researchers due to the close relation of its chromosomes with the D-genome of hexaploid wheat as well as the variety of useful genetic diversity it contains. This diploid has been associated with resistance to leaf rust and stem rust (Kerber & Dyck, 1978; Yamashita & Tanaka, 1968; Gill et al., 1986; Cox et al., 1992), powdery mildew (Potokina & Yusupbaeva, 1982; Cox et al., 1992), yellow rust (Appels & Lagudah, 1990), tan spot (*Pyrenophora tritici-repens*) (Cox et al., 1992), *Septoria nodorum and S. tritici* (Appels & Lagudah, 1990). The studies of Cox et al. (1992) and Appels & Lagudah (1990) involved 219 and 420 *T. tauschii* accessions, respectively.

Niemeyer (1988) adopted a different approach in exploring the genetic resource of *Triticum*. He measured the hydroxamic acid concentration of plant tissues. Hydroxamic acid is a secondary metabolite thought to be associated with pest and disease resistance in plants. Hydroxamic acids were found in all accessions (17 *Triticum* species including former *Aegilops* species, in total 55 accessions), with extreme values in the wild diploids.

1.7.2.2. Resistance to insects, nematodes and viruses

Sources of resistance to the cereal cyst nematode (Eastwood et al., 1991; Appels & Lagudah, 1990) and the wheat curl mite (Thomas & Conner, 1986) were identified among 420 *T. tauschii* accessions.

Genetic resources of resistance (antibiosis) to biotypes D and C of the Hessian fly were found among *T. tauschii* accessions. The resistance gene products interfere with larval feeding, causing the death of the larvae (Hatchett & Gill, 1981, 1983; Gill et al., 1985, 1986). Resistance to the Hessian fly among accessions of *T. araraticum* was also reported by Gill et al. (1986).

Greenbug resistance has been identified in 7 *Triticum* species (10 accessions) following the screening of 17 *Triticum* (formerly *Aegilops*) species (53 accessions) (Gill et al., 1985). Greenbug resistance has also been detected in *T. tauschii* by Gill et al. (1986) and Harvey et al. (1980).

Resistance to BYDV (barley yellow dwarf virus) has been detected among 349 accessions of 20 *Triticum* (formerly *Aegilops*) species with 34 accessions from 13 species being resistant. In the resistant plants the virus concentration was found to be either extremely low or non detectable (Makkouk & Ghoulam, 1991).

1.8. Gene transfer from other *Triticum* species to common wheat

Wheat is a crop species in which alien genetic variation has been exploited frequently. The hexaploid condition allows common wheat to tolerate unbalanced genetic constitutions, making it suitable for this type of genetic transfer. Resistance to a variety of fungal diseases, viral diseases, and insect pests as well as tolerance to abiotic stresses have been transferred to wheat from wild and primitive relatives (Sharma & Gill, 1983; Feldman, 1988; Knott, 1987; Jiang et al., 1994).

Although wild wheats constitute the homologous gene pool, their use in wheat breeding has been rather limited (Sharma & Gill, 1983). Common difficulties associated with gene transfer from the homologous gene pool are: cross-incompatibility, sterility caused by differences in ploidy level, occurrence of complementary genes causing seedling lethality and yield potential impairment (Gill et al., 1983). More importantly, frequent alteration, reduction or suppression of the level of gene expression during the transfer to common wheat occurs (Knott, 1978; Dyck, 1982; Kerber, 1983; Gustafson & Dera, 1989; Bai & Knott, 1992). Most work on the incorporation of characters from alien germplasm resources has dealt with disease resistance because of their simple inheritance mechanisms (Damania, 1991).

1.8.1. Gene pools in the Triticeae

The wild relatives of wheat may be grouped into primary, secondary and tertiary gene pools (Fig. 6). This classification generally reflects the ease of accessibility and utilization for crop improvement of the genetic resources and is based on their genomic constitutions.

The primary gene pool in the tribe consists of biological species between which gene transfer can readily be achieved by means of direct hybridization, homologous chromosome recombination, backcrossing and selection (Bothmer et al., 1992; Jiang et al., 1994). Occasionally the production of the hybrid F_1 may require the application of an embryo rescue technique. The group includes the hexaploid land races, cultivated and wild tetraploids of the *turgidum* group, and the diploid progenitors of the A- and D-genomes (Table 1 & 6).

The secondary gene pool represents the closely related *Triticum* species from whose members gene transfer is difficult, but possible. These include the diploid, putative B-genome donors of the former *Aegilops* Sitopsis section (Table 6) and the polyploids which share a common genome with hexaploid wheat (Table 6). Genes located on a homologous genome can be transferred by the procedure described for genes from the primary gene pool (see above). However, genes located on a homoeologous genome will require special cytogenetic procedures similar to those that are generally required to transfer genes from the tertiary gene pool (Table 7).

The tertiary gene pool consists of species from which gene transfer is very difficult. The pool includes all species which have non-homologous, but often homoeologous genomes (Table 6). Introgression cannot be achieved through recombination in these transfers. However, it may be possible to induce homoeologous chromosome pairing and recombination using special cytogenetic techniques. Otherwise, gene transfer may be achieved through ionizing irradiation (Table 7) or the prolonged propagation of tissue calli.

Kimber (1993, in Mujeeb-Kazi & Wang 1995) considered genome relationships to construct a table listing the potential donor species in the genus *Triticum*. Drawing on the literature, he provided a summary of the most sensible transfer technique to employ in each case, the likelihood of success and possible problems that may arise. This information is provided here in a slightly modified way as Table 7.

1.8.2. Introduction of alien genetic variation to wheat

A number of considerations apply to the introduction of an alien genetic variation into common wheat.

(i) *Identification of a donor for the target character*. This requires firstly access to wild species collections, and secondly, the availability of an effective screening technique which will allow for the clear recognition of the character in question.

(ii) *Genetic complexity of the character*. The higher the degree of complexity the less successful the transfer might be (e.g. physiological and quantitative characters are most probably affected by many genes and the successful transfer will be difficult).

(iii) *Crossability*. Parental wheat genotypes that are crossable with the donor species are required.

(iv) *Phenotypic expression of the character in the recipient background*. The gene under transfer should not be suppressed by the wheat genetic background.

(v) *Level of chromosome pairing in the hybrid*. Once desirable variation has been identified in an alien species and its expression in the hybrid has been confirmed, then the choice of methodology for the introduction of the gene(s) follows logically from the criterion for relative affinity of the chromosomes involved (Table 7).

1.8.3. Production of F_1 hybrids in wide crosses

The production of a F_1 hybrid is the first step towards the introduction of an alien genetic variation. This was extensively shown as being achievable if advantage is taken of procedures such as: the identification of highly crossable wheat genotypes and the correct parental combination, use of hybridizing agents, premature (early or bud) pollination, reciprocal and bridging crosses, chromosome doubling of the wild parent and embryo rescue (Sharma & Gill, 1983; Hadley & Openshaw, 1980; Sears, 1981; Mujeeb-Kazi & Kimber, 1985). Nevertheless, reproductive isolation barriers evolved during the process of speciation to maintain species integrity by restricting the gene flow between them. While some of these barriers, may be overcome in the parental species during hybridization, further barriers as hybrid weakness or inviability, failure of flowering, hybrid sterility, hybrid breakdown, hybrid necrosis and chlorosis may appear subsequently (Hadley & Openshaw, 1980; Valkoun et al., 1990).

Phylogenetic relationships should be considered during introgression. Generally, as the phylogenetic distance increases so does the difficulty of introducing alien genetic material. Thus, it becomes necessary to resort to manipulations of the chromosome-pairing regulation systems in order to induce chromosome pairing and recombination. When the relationships become so remote that this is no longer possible, methods causing chromosome breakage and reunion, such as ionizing radiation and somaclonal variation, are to be attempted.

1.8.3.1. Crossability of the wheat parent

A wide range of genetic variation for crossability with their wild relatives exists among the wheat cultivars and landraces (Zeven, 1987; Farooq et al., 1990; Luo et al., 1992; Farshadfar et al., 1994). So far at least four genes for crossability, designated *kr*, have been identified. Till recently the wheat cultivar "Chinese Spring" (CS) was considered to be the most crossable wheat genotype (Jiang et al., 1994). It contains three of the four known *kr* genes that enhance crossability, i.e. the recessive genes *kr*1, *kr*2 and *kr*3 located on homoeologous chromosomes 5B, 5A and 5D, respectively (Falk & Kasha, 1983). The fourth gene, *kr4*, has been found in 16 landraces from the Sichuan Basin, China (Farshadfar et al., 1994; Jiang et al., 1994), the same region where CS originated (Yen et al., 1988; Sears, 1988). The added presence of this gene, located on chromosome 1A (Luo et al., 1993; Farshadfar et al., 1994; Jiang et al., 1994), to the *kr*1, *kr*2 and *kr*3 genes was found to produce levels of crossability with rye that were higher than that of CS. Moreover, one specific line "J-11", was recently reported to produce hybrids with species as distantly related to wheat as *Psathyrostachys huashanica*, *Roegneria ciliaris* and *Hordeum*

bulbosum (Luo et al., 1993). The same line achieves a crossability of 16.49% with *T. tauschii* (Luo et al., 1993) compared to 2.08% for CS (Farooq et al., 1990).

1.8.3.2. Premature pollination

Difficulty experienced in the production of a particular hybrid can often be overcome by crossing a wide range of parental genotypes or by crossing in the reciprocal combinations. Sometimes, crossability barriers may be overcome by changing the conventional pollination timing in favour of premature (early or bud) pollination. Pollinations are then made before there are any indications of receptiveness of the stigma (Mujeeb-Kazi & Kimber, 1985; Mujeeb-Kazi & Asiedu, 1990). The procedure seems to escape barriers to fertilization that develop as the stigma matures. In this way Mujeeb-Kazi et al. (1984) obtained hybrids in previously unsuccessful crosses.

1.8.3.3. Hybridizing agents

The use of hybridizing agents involves mainly the application of immuno-suppressants (Mujeeb-Kazi & Kimber, 1985) and normal growth promoters such as gibberellic acid (GA) (Larter & Chaubey, 1965) and 2,4-dichlorophenoxyacetic acid (2,4-D) (Kruse, 1974; Sharma & Gill, 1983; Inagaki, 1990). Chemical treatments may be done prior to pollination with the intention of overcoming incompatibility barriers, promoting pollen-tube growth and improving gynoecium longevity and delivery of the male gametes (Larter & Chaubey, 1965; Hadley & Openshaw, 1980; Mujeeb-Kazi & Kimber, 1985). Post-pollination treatment with hybridizing agents is generally aimed at manipulating and promoting the growth of embryos until they are large enough to be cultivated on artificial media (Mujeeb-Kazi & Kimber, 1985). It has been demonstrated by Kruse (1973) that a single application of 75ppm GA_3 in the post-pollination period effectively assists the developing embryo. Increased seed set has also been achieved by the direct injection, post-pollination, of 2,4-D solutions into culms (Inagaki, 1990).

1.8.3.4. Reciprocal crosses

It is not uncommon to find that crossability differs when reciprocal crosses of two species/genera are made (Knott, 1989b). It is sometimes necessary to try reciprocal crosses, especially when there is uncertainty about the crossability of the two parents, when incompatibility exists between the embryo and the endosperm, or when somatoplasmic sterility occurs (Hadley & Openshaw, 1980; Knott, 1989b). The use of the wild species as female parent in crosses with common wheat often results in some of the above mentioned problems, for example, cytoplasmic male sterility often results following the transfer of the wheat genomes into an alien cytoplasm. This problem may sometimes be overcome if the hybrid produces some fertile pollen which can be used in a backcross to wheat. If that is not the case, a number of backcrosses to different cultivars may be attempted in an effort to find one that carries fertility restoring genes.

1.8.3.5. Bridging crosses

Problems with fertility may arise if the wild species and wheat parents differ widely with regard to their chromosome numbers. Use of a bridging parent with an intermediate ploidy level may alleviate the problem. The classical example of this procedure was its use by Sears (1956) to transfer a gene for leaf rust resistance from *T. umbellulatum* (genomes UU) to common wheat (AABBDD) using *T. dicoccoides* (AABB) as the bridge species.

1.8.3.6. Chromosome doubling

Induced chromosome autoduplication provides another means of overcoming crossability barriers due to variation in the ploidy levels of the parents. Although chromosome doubling is not readily achievable, the procedure adds the advantage that the F_1 may provide restitution nuclei so that the B_1F_1 seeds will then be amphiploids (Mujeeb-Kazi & Asiedu, 1990).

1.8.4. Embryo rescue and culture

Embryo rescue and culture are aimed at removing the embryo aseptically as late as possible in its development, but still early enough to allow its continued development on artificial media.

In many interspecific and intergeneric hybrids endosperm degeneration may start very early and seems to be closely related to the cessation of embryo growth (Knott, 1989b). The reason is probably embryo/endosperm incompatibility following wide hybridization. Often, embryo development tends to slow down about a week or so after pollination and in 10 - 14 days the embryo may cease to develop (Mujeeb-Kazi & Kimber, 1985). However, for plant material grown under greenhouse conditions most embryo rescues are accomplished around 18 days after pollination (Table 8). The earlier embryo-rescue operations have to face the more complex nutritional requirements of the excised embryo, and therefore are rarely successful. The more mature the embryo, the better autotroph it is, thus requiring simpler nutrient media (Poehlman, 1987). Currently, the most frequently used media for embryo culture in the Triticeae are modifications of Murashige & Skoog's (1962) basic media, as well as, the media described by Gamborg et al. (1968) and Taira & Larter (1978). The production of mature plants from hybrid embryos may sometimes be very difficult, yet should not be a constraint, because some level of compatibility has already been demonstrated by the fact that sexual fusion has taken place. Therefore, it would seem that an improvement in the embryo-rescue technique and nutrient media formulation will largely benefit attempts to transfer alien genetic material found in the related species.

1.8.5. Hybrid disorders

1.8.5.1. Hybrid weakness or inviability

In spite of the ability of parental species to produce hybrid zygotes, the hybrid F_1s may suffer from inviability or weakness. Often the hybrid plants become grassy and clumped in appearance, remaining in the vegetative stage and not being able to form reproductive organs (Valkoun et al., 1990). This is most probably caused by one of the following types of disharmonies: i) between

the genomes of the parental species, ii) between the genome of one parent and the cytoplasm of the other, or iii), between the genotypes of the F_1 zygote and maternal endosperm tissue (Hadley & Openshaw, 1980). Hybrid weakness is probably a reflection of the differences acquired during the evolution of the species and the timing of their tissue development processes, namely, meristem formation, organization and differentiation, cell division, germination, etc. These genome interactions may prove to be highly parent dependent, therefore alternative parental combinations, including reciprocal and bridging crosses need to be considered. Generally speaking though, crosses between species differing in ploidy level and/or chromosome number are more successful when the higher number/level is used as the female parent.

1.8.5.2. Hybrid sterility

Characteristically, most interspecific hybrids of wheat and *Triticum* species have reduced chromosome pairing, complete male sterility and a high degree of female sterility (Maan, 1983). This F_1 hybrid sterility has been accredited to structural differences in the chromosomes of the related species resulting in impaired meiosis which produces non-functional gametes or zygotes. This results in two types of hybrid sterility, "chromosomal", due to chromosomal structural differences between the species genomes, and "genic", caused by specific gene complexes (Hadley & Openshaw, 1980). The lack of chromosome homology, unstable meiosis and the production of chromosomally unbalanced and non-functional gametes in the hybrid F_1s can be attributed to chromosomal structural heterozygosity, since these can be corrected in the amphiploids. Thus, the difference between "genic" and "chromosomal" hybrid sterility becomes visible in the fertility of the amphiploids. With "chromosomal" hybrid sterility the amphiploids have restored fertility and normal meiosis, while "genic" sterility persists in the amphiploids even though they may have stable meiosis.

1.8.5.3. Hybrid breakdown

Hybrid breakdown or genetic disability occurs when the F_1 proves to be both vigorous and fertile but still gives rise to weak or sterile F_2 plants. The condition may originate during meiosis in the hybrid F_1 when, as a result of the recombination of chromosome segments involving structural differences, abnormal gametes escape elimination and produce abnormal F_2 or later generation sporophytes (Hadley & Openshaw, 1980).

1.8.5.4. Hybrid necrosis and chlorosis

There are two known types of genetically controlled hybrid disorders in the polyploid wheats. They are the result of interactions between pairs of complementary dominant genes that occur on wheat chromosomes (Tsunewaki & Hamada, 1968).

Hybrid necrosis (Ne) occurs in the F_1 of crosses between hexaploid wheat cultivars or crosses between hexaploid wheat cultivars and tetraploid emmer wheats (Tsunewaki, 1992; Worland et al., 1987) The cause is the two genes *Ne1* and *Ne2*, located on chromosome arms 5BL and 2BS, respectively. Multiple allelic series exist at both loci. The necrosis affects the older leaves first

and starts to develop from the leaf tip resulting in premature death of leaf blades and sheaths. The severity may vary from slight dwarfing and yield reduction to premature death of the entire plant.

Hybrid chlorosis (Cs) is known to occur only in the hybrids of common wheat crossed with certain emmer wheats or a range of *timopheevii* wheats, both wild and cultivated (Tsunewaki & Nakai, 1973; Tsunewaki, 1992). It is caused by the genes *Cs1* located on chromosome 5A and *Cs2* located on chromosome 4D of wheat (Tsunewaki, 1992). The symptoms of chlorotic discoloration may appear at different growth stages, in accord with the parents involved in the cross (Worland et al., 1987).

1.9. Production of amphiploids

The production of amphiploids is a prerequisite for successful gene transfer in many wide crosses for the following reasons: i) to restore fertility in highly sterile hybrid, ii) to allow for a reliable evaluation of the expression of alien genes in the genetic background in the wheat recipient, iii) to serve as a permanent resource for the detection and transfer of new characters, iv) to help overcome nucleo-cytoplasmic incompatibility in the later generations of alloplasmic hybrid (by serving as a male parent in the first backcross to wheat), etc. (Jiang et al., 1994). Though highly desirable, amphiploid production is generally difficult and the end products are not always genetically stable.

The conventional method for amphiploid production involves the treatment of the F_1 hybrids with antimitotic agents, thus doubling their chromosome numbers. Colchicine treatment is the most frequently employed technique for inducing autoduplication, although other procedures are also available (Gale & Miller, 1987; Hadley & Openshaw, 1980; Inagaki, 1990). Colchicine is used mostly as an aqueous solution in concentrations from 0.05-0.3% with the time of exposure varying from 3-72 hours. Additives such as dimetyl sulfoxide (DMSO) (1.5-2%), a wetting agent such as Tween 20 (15 drops/l) and GA_3 seemingly increase the effectiveness of the treatment (Winkle & Kimber, 1976; Thiebautt & Kasha, 1978). The solution is applied predominantly to the root area, but immersion of the crown is not uncommon. When there is a need for prolonged exposure or an aqueous solution is impractical, lanolin paste mixture can be applied. The treatment is directed at the meristem tissue and generally it must cause some tissue damage in order to be effective. This necessitates careful handling of the treated plants, thorough washing of the exposed plant parts to remove any residue, and post-treatment incubation at low temperature (4^0C is adequate) for up to 72 hours prior to potting (Pienaar, personal communication). The tissue that develops after the treatment is normally mixoploid and because of natural selection within the plant, the original rather than doubled cells are retained. The polyploid tissue therefore needs to be selected. Valkoun et al. (1990) reports an alternative treatment involving direct injection of a solution of 0.1% colchicine, 2% DMSO and 0.001 GA_3 into the top internode. Colchicine may also be applied via the medium during the culture stage in some applications (Valkoun et al., 1990). While amphiploidisation may occur naturally or may follow chemical induction procedures, recent work by Xu & Dong, (1992) showed that certain subspecies of *T. turgidum* (*persicum* and *durum*) when used as female parents cause spontaneous amphiploidization

of the F_1. If a simple genetic system is responsible, it may be possible to transfer the gene(s) involved to common wheat in order to facilitate introgression attempts.

1.10. Transfers involving homologous genomes

The homologous genome group includes all wild species sharing a common genome with wheat (see Table 6). These include the descendants of the donor species of the A- and D-genomes (*T. monococcum* and *T. tauschii*) as well as the wild members of the *turgidum* family (AABB). Several other polyploid *Triticum* species share an A- or D-genome with common wheat. Among them, the wild and cultivated forms of *T. timopheevii* (AAGG) occupy an intermediate position regarding genome homology, with one genome being homologous (A) and the other (G) 47% similar to the B-genome (Salle & Kimber, 1978; Kimber et al,. 1981). Gene transfer between the representatives of the homologous genome group and common wheat may be achieved readily through normal crossing over, since in most cases complete pairing can be expected between their shared chromosomes. In introgressions of this type failure of some genes to express in the hexaploid wheat background may occur, due to suppressor genes on wheat chromosomes such as 7DL (Kerber, 1983, 1991), 1D, 2D and 4D (Bai & Knott, 1991). A mutation of the genetic suppressor on 7DL has been found which allowed expression of three recessive genes for resistance to stem rust (Williams et al., 1992).

1.10.1. Transfers from A- and D-genome diploids

Hybridization of common wheat and its diploid progenitors, *T. monococcum* (*T. urartu*) and *T. tauschii* is not easy to achieve and the hybrids are highly sterile (Farooq et al., 1990; Feldman, 1988; Innes & Kerber, 1994). Nevertheless, if the hybrid F_1 can be successfully backcrossed using wheat as the male parent, the progeny is usually more fertile and recurrent backcrossing is expected to result in the introgression of desirable genes to the parental A- or D-genoms (Vardi 1973; Alonso & Kimber, 1984) (Fig. 7A).

As an alternative strategy, *T. turgidum* (AABB) may be crossed as a female bridging species with *T. tauschii* and the chromosome number of the hybrid F_1 doubled to produce a 42-chromosome synthetic hexaploid (Fig. 7B) (Sharma & Gill, 1983; Mujeeb-Kazi & Asiedu, 1990). The latter plant can then be crossed with and backcrossed to common wheat. Another alternative is to extract the AABB genomes of a commercial *T. aestivum* cultivar and then to cross the derived synthetic tetraploid with *T. tauschii* to develop a synthetic hexaploid after chromosome doubling (Fig. 7C) (Mujeeb-Kazi, 1995).

An alternative procedure to introgress genes from *T. monococcum* entails autotetraploidization and subsequent hybridization with, and backcrossing to hexaploid wheat (Dyck & Bartos, 1994; Gerechter-Amitai & Stubbset, 1970). Another possibility might be to cross the autotetraploid (AAAA) with durum wheat and to backcross it once or twice to durum wheat before crossing and backcrossing the latter hybrid with common wheat (Knott, 1987, 1989b).

1.10.2. Transfers from AB tetraploids

In general, the wild AB tetraploids are cytogenetically very closely related to the cultivated wheats. The two groups cross readily and yield fully fertile F_1 hybrids (Feldman, 1988). When wild AB tetraploids are crossed with hexaploid wheat, at least one of the reciprocal crosses will produce partially fertile hybrids with a fairly high amount of chromosome pairing (up to 14" and 7') (Knott, 1989b). The hybrid then has to be backcrossed several times to the recurrent hexaploid parent in order to recover plants with 21", showing the parental genotype. Although backcrossing will reduce the possibility for transfer of linked deleterious genes, a block of species derived genes will remained linked to the desired one. The breaking of this linkage block may prove difficult if the homology between the parents is incomplete.

1.10.3. Transfers from A and D polyploids

Transfers from A- and D- genome polyploids to cultivated tetraploid or hexaploid wheats can be attempted either by direct crossing or via the production of suitable amphiploids. Backcrossing of the primary F_1 may eventually result in the formation of some seeds. With continued backcrossing, extensive exchanges between the common genomes, A or D, are expected. In this way a number of transfers were made from the most extensively used A- and D-genome polyploids, i.e. *T. timopheevii* and *T. ventricosa*. Through direct crossing genes for resistance against leaf rust, stem rust and powdery mildew were derived from *T. timopheevii* (Knott, 1987, 1989c; Sharma & Gill, 1983) and genes for resistance to eyespot from *T. ventricosum* (Doussinault et al., 1988; Delibes et al., 1988). Eyespot resistance could also be transferred from *T. ventricosum* using *T. turgidum* as a bridge (Jahier et al., 1978; Delibes et al., 1988). In crosses of common wheat with *T. timopheevii*, F_1 hybrids are generally easy to obtain. However, male sterility that persists even after one or more backcrosses is often experienced (Knott, 1987).

1.11. Transfers involving homoeologous genomes

The homoeologous genome group of wheat relatives possesses a wide range of useful characters. Although it does not have homology with wheat, a number of methods make it possible to achieve homoeologous chromosome recombination resulting in introgression. The production of alien addition and substitution lines is an important starting point to achieve the so-called precise transfers, which involve less than an entire alien chromosome (Feldman & Sears, 1981). In these procedures the alien addition and substitution lines serve as "bridging materials to generate wheat-alien chromosome translocations" (Jiang et al., 1994).

1.11.1. Aneuploid wheat stocks

Deviation from the euploid (2n) chromosome number is referred to as aneuploidy. It occurs most frequently in the polyploid species, whose genome multiplicity provides a degree of compensation for any chromosome loss or gain. As a result a wide range of aneuploids can survive in the polyploid species. Very diverse and complete sets of aneuploids were collected in common wheat for the purpose of genome analysis and manipulation (Table 9).

Sears produced complete sets of all 21 possible nullisomics, monosomics, trisomics and tetrasomics in common wheat (Sears, 1988). The original aneuploids were selected among the progeny of either haploid or nullisomic 3B plants (the latter being partially asynaptic) of the cultivar Chinese Spring. Misdivision of monosomes gave rise to the 42 different telocentrics and 13 different isochromosomes (with two identical arms). From these a variety of other aneuploid types were derived (see Table 9). The wealth of aneuploids, particularly monosomics and telocentrics, were utilized extensively for the identification of chromosomes carrying particular genes and to map genes relative to the centromeres (Knott, 1989d). The aneuploids are also important tools for the production of wheat-alien substitution lines and the manipulation of the homeologous pairing mechanism for the induction of chromosome recombination and alien introgression.

1.11.2. Wheat-alien addition lines

A wheat-alien chromosome addition line possesses the full complement of chromosomes of a cultivated wheat plus one pair of chromosomes from a wild relative (Feldman & Sears, 1981). An addition line can be produced by crossing the alien donor species with wheat and backcrossing either the polyhaploid F_1 or the amphiploid to the wheat parent while simultaneously selecting for the target character (Fig. 8a,b) (Sears, 1981; Feldman & Sears, 1981; Knott, 1987, 1989b)

When difficulty is encountered in crossing a diploid alien species to common wheat as a result of differences in ploidy level, a bridging species can be employed (Fig. 8c) (Gale & Miller, 1987).

An alternative procedure for the production of disomic addition lines is to pollinate monosomic addition plants with *Hordeum bulbosum* (Barcley, 1975) or *Zea mays* (Laurie & Bennett, 1986) (Fig. 8d). In these crosses total elimination of the alien (*bulbosum*, *mays* etc.) genome occurs during the early embryo and endosperm divisions resulting in the development of a haploid. Haploid plants that express the desired gene and which have 3x+1 chromosomes are identified. Following chromosome doubling a polyhaploid disomic addition line is produced.

The addition of an alien chromosome pair rarely, if ever, leaves the genotype well balanced. Pollen selection does not favour alien chromosomes and results in a tendency of the line to revert to the more stable euploid condition (Sears, 1981). Consequently, cytological maintenance is required at each selfing generation (Gale & Miller, 1987).

1.11.3. Wheat-alien substitution lines

An alien substitution line has a pair of alien chromosomes substituted for a pair of homoeologous wheat chromosomes (Feldman & Sears, 1981). A substitution line is most often, but not always, produced from an alien addition line. If the homoeology of the addition chromosomes to the wheat chromosomes is not known, the addition line is usually crossed with the monosomics for the seven homoeologous groups of wheat chromosomes. The ability of an alien chromosome to compensate for the loss of a wheat chromosome is then used as an indicator of homoeology. Thus, only the homoeologous substitutions will result in the recovery of fertile and vigorous

plants (Feldman & Sears, 1981; Gale & Miller, 1987). Genetic markers may also provide a means for determining the homoeology between the individual wheat chromosomes and the alien chromosomes in question (Sharp et al., 1989) thus eliminating the need for unnecessary crosses.

Occasionally, monosomic substitutions (20"+1'+1'A) occur naturally during backcrossing and upon selfing can produce disomic substitutions (20"+1"A). A number of methods have been reported for producing wheat-alien substitution lines (Fig. 9).

Substitutions can be produced by crossing a specific wheat monosomic with an alien addition line. The progeny is expected to be either 21"+1'A (alien chromosome) or 20"+1'+1'A. Following selfing of the 20"+1'+1'A plants, both additions and substitutions are produced. Substitution will be easier to achieve if the alien chromosome is homoeologous with the missing wheat chromosome (Fig. 9a) (Sears, 1981).

Alternatively, the wheat monosomic can be pollinated by 20"+1'+1'A plants. If the alien chromosome substitutes well for the monosomic wheat chromosome, 20'+1'A pollen will function and F_1 plants with 20"+1'A will be produced. After selfing these plants, disomic substitutions can be produced (Fig. 9b) (Knott, 1987, 1989b).

Another alternative is to pollinate 20"+1'+1'A plants with an alien addition line. With no selection expected against the alien chromosome in the female parent, approximately 3/8 of the egg cells should be 21'+1'A. Approximately 50% of the F_1 plants should then be 20"+1'+1"A. Selfing these plants can give rise to a substitution line even if male transmission of the alien chromosome is poor (Fig. 9c) (Knott, 1987, 1989b). Due to the tendency for misdividion in the alien addition monosome, telosomic additions can often be obtained in the process (Sears, 1981).

Substitutions can also be produced by crossing a specific wheat monosomic with a ditelo alien addition line. From the expected progeny, either 21"+t'A or 20"+1'+t'A, selfing of the 20"+1'+t'A plants will produce both additions and substitutions (Fig. 9d) (Gale & Miller, 1987).

A technique for the production of wheat-alien substitution lines which avoids the initial production of addition lines has been suggested by Kota & Dvorák (1985). The technique involves crossing monotelosomic (20"W+t') wheat plants and the diploid alien species (7"A), to produce two types of allohaploid progeny, i.e. 20'W+t'+7"A and 20'W+7'A. Following chromosome doubling of the latter plant, the amphiploid (20"W+7"A), is backcrossed as the male parent to the monotelosomic. The wheat chromosome missing in the nullisomic amphiploid is likely to be substituted by its homoeologue from the alien diploid. This will result in the rapid loss of the nonhomoeologous alien chromosomes through selection during backcrossing but the retention of the appropriate homoeologue.

Zhang et al. (1992) provided yet a further alternative. An alien amphiploid is produced at first and used to pollinate the fertile wheat nullisomics. This is followed by backcrosses of the hybrids to the nullisomic line (male parent). Thus, the missing wheat chromosome in the nullisomic line will be substituted by its alien homoeologue from the amphiploid.

1.12. Spontaneous translocations

Homoeologous gene transfers often involve spontaneous translocations. This can occur in the derivatives of wheat-alien hybrids following hybridization and subsequent backcrossing, when the wheat and alien chromosomes may recombine, albeit at very low frequency (Jiang et al., 1994). Another class of spontaneous homoeologous translocations occurs when wheat and homoeologous alien chromosomes are simultaneously present as univalents during meiosis. So-called Robertsonian's translocations may occur that involve wheat and alien chromosomes and which arise from misdivision (centromeric breakage) and centric fusion (Sears, 1972). Non-Robertsonian's translocations involve non-centromeric breakage and fusion and are much rarer (Miller et al., 1988). Conditions conducive to misdivision and reunion can be simulated in hybrids by creating combinations having univalents of appropriate wheat and alien chromosomes (Sears, 1972, 1981).

1.12.1. *Ph*-based wheat-alien translocations

This approach is based on the manipulation of the *Ph* (pairing homoeologous) genetic system in wheat that serves to suppress homoeologous chromosome pairing. Thus far, incomplete suppression of homoeologous pairing has been achieved by deleting the chromosomes (5B and 3D) that carry the *Ph1* and *Ph2* genes, by deleting the *Ph* genes themselves, or by suppressing their action. These manipulations are possible through the use of aneuploidy, mutation or a genetic system able to suppress the action of the *Ph* system. These procedures became possible after it was discovered by Sears & Okamoto in 1958 (Sears, 1981) that meiotic chromosome pairing in wheat is under genetic control. The role of the *Ph* control mechanism is to provide diploid-like pairing in hexaploid wheat by suppressing meiotic pairing between the chromosomes of the homoeologous genomes A, B, and D. In this way the *Ph* genes ensured genome stability and fertility during the evolution of polyploid wheat (Chen et al., 1994). However, in the absence of the *Ph* genes homoeologous pairing and recombination can occur. This observation led to the utilization of *ph*-induced chromosome pairing for the transfer of a number of agronomically important genes (Knott & Dvorák, 1976; Sears, 1981; Knott, 1978, 1987, 1989; Merker, 1992).

The *Ph* system involves one major gene, *Ph1*, on 5BL which has the most pronounced effect, an intermediate-pairing gene, *Ph2* on 3DS, and a number of genes with minor effects that may either suppress or promote homoeologous pairing (Sears, 1976; Feldman & Sears 1981). Such genes have been found on a number of chromosomes (e.g. 5D, 5BS, 5AL, 3D). Chromosomes 3BL and 2AS were found to also carry genes that are essential for normal chromosome pairing.

The main advantage of the *Ph*-induced translocations is that directed exchanges of genetic material involving specific alien and wheat chromosomes are possible. Nevertheless, careful consideration is necessary before determining the recipient wheat chromosome. In this respect the use of structurally modified chromosomes (such as 4A, 5A and 7B that are involved in cyclical translocations), chromosome arms possessing fertility genes (6BS) or genes involved in the diploidisation of the wheat genome (2AS, 4BS) as well as those chromosomes that carry major *Ph*

genes (3DS, 5BL), should be avoided as recipients for alien chromosome translocations, because this may hamper fertility and genome stability (Jiang et al., 1994).

1.12.2. Crosses with wheat lines deficient for the *Ph*1 locus

Alien gene transfer by *ph*-induced chromosome pairing and chromosome recombination can be achieved by crossing either the alien species, a synthetic wheat-alien amphiploid or an alien addition or substitution line to an aneuploid deficient for the *Ph1* locus on 5BL (Fig. 10). Wheat aneuploids suited to this purpose are: monosomic 5B (M5B), monotelosomic-5BL (Mt5BL) nullisomic-5B tetrasomic-5D (N5BT5D) or nullisomic-5B tetrasomic-5A (N5BT5A) (Sears, 1984; Feldman, 1988). Upon crossing, F_1 progeny is produced that is deficient for *Ph1*, and homoeologous pairing is expected to take place during metaphase I (Sears, 1981; Feldman, 1988). A problem encountered with 5B-deficient hybrids is their low fertility, but as long as the progeny is at least female fertile, a backcross to wheat can recover the crossover chromosomes (Sears, 1981; Knott, 1987).

1.12.3. Crosses involving *ph* mutants

In an attempt to use the condition of disrupted homoeologous pairing more effectively, work was undertaken aiming to produce high-pairing mutations at the *Ph* loci (Sears, 1984). Attempts to induce mutations at the *Ph* loci by means of ionizing radiation or chemical mutagens turned out to be successful in a number of studies (see Sears, 1976), but the recovery of the mutations proved not to be an easy task. Nevertheless, after a number of attempts by various workers, Wall et al. (1971), recovered a mutant which they allocated to chromosome 5BL. The mutant was thought to be an allelic variant rather than a deletion of *Ph1* since its homozygous condition allowed less homoeologous pairing than the nulli 5B condition. The mutant was designated *ph1a*, but was later found to be a mutation of the *Ph2* locus on 3D and renamed *ph2a* (Sears, 1976, 1981, 1984). A mutant deficient for *Ph1*, and equal in effectiveness to the nulli 5B condition was recovered by Sears in 1975 (Sears, 1976). Homozygotes for the mutation had reduced vigour and fertility, but the male transmission of the deletion was fairly normal. This mutation was named *ph1b*. A third deletion was reported by Sears (1977, 1982). This mutation occurs at the *Ph2* locus on chromosome 3D and was designated, *ph2b*. A *ph*-mutant was also induced in durum wheat and is thought to be a deletion of *Ph1* (Knott, 1978). Generally the *ph* mutants, and in particular *ph1b*, induce a high level of homoeologous pairing in stocks homozygous for the mutation. As a result unbalanced gametes are formed which may cause a variable degree of sterility (Sears, 1981; Feldman 1988; Knott, 1989b). For this reason *ph*-stocks are best maintained as heterozygotes (Knott, 1989b). As the *ph* mutants are recessive, their homo- or hemizygous condition is required in order to induce homoeologous pairing in a particular hybrid (Knott, 1987). Due to the "extremely low fertility" of the hybrid F_1 of a wide cross, the direct cross approach between a *ph* line and an alien species should be avoided. Preferably the first cross should be made with a highly crossable wheat genotype such as CS, and the F_1 should then be backcrossed to the *ph* line (Sears, 1981; Sharma & Gill, 1986).

In order to produce exchanges between closely-related homoeologues (e.g. S- and B-genomes), the less effective *ph2a* or *ph2b* mutants can be used instead of *ph1b* (Sears, 1981; Feldman, 1988). The use of a wheat-alien addition line is preferable as it is easier to manipulate a single alien chromosome than an entire alien genome (Gustafson & Dera, 1989). A precise method of introgression would be to start with a wheat-alien substitution line (Fig. 10) (Sears, 1981, 1982, 1983; Gale & Miller, 1987; Feldman, 1988; Knott, 1987). From such a line, plants can be produced that are monosomic for both the alien chromosome and one of its wheat homoeologues, as well as deficient for *Ph* (Gustafson & Dera, 1989). This will ensure that most of the homoeologous pairing will take place between the alien and known wheat monosome.

1.12.4. Crosses with species carrying a suppressor of *Ph*

It has been found by different workers that certain genotypes of the diploid species *T. speltoides*, *T. tripsacoides*, *T. longissimum*, *T. umbelullatum* and *T. dichasians* have the effect of promoting homoeologous chromosome pairing in wheat (see Sears, 1976). The level of pairing induced by the high-pairing genotypes of *T. speltoides* and *T. tripsacoides* equals that produced by a deficiency for 5B. The effect of *T. umbelullatum* chromosome 5U was reported to be similar to the effect of the promoter on 5D. The mechanism of action of the *T. dichasians* genomes is to partially suppress the *Ph* mechanism in its hybrids with common wheat. The existence of a *Ph* suppressor system in some diploids can be utilized for the induction of homoeologous pairing and chromosome translocation. This can be accomplished by crossing a high-pairing genotype such as *T. speltoides* with an alien species, a synthetic amphiploid, an addition or substitution line. Homoeologous pairing is expected to occur in the resultant F_1. This is followed by crosses with, and several backcrosses to the wheat parent, accompanied by selection for the desired character (Knott, 1987, 1989). Recently, Chen et al. (1994) reported the transfer of Ph^I (inhibitor) genes from *T. speltoides* to common wheat, which confer a high level of homoeologous pairing. Since the genes are epistatic to the *Ph* genes and are also dominant, they cause homoeologous pairing in the F_1 hybrids. This allows for easier transfer of alien genetic material to wheat than does the recessive *ph1* mutant or the nullisomic-5B (N5B) condition. Another advantage to the use of Ph^I genes, rather than the entire *T. speltoides* genome, is that it avoids the introduction of undesirable *speltoides* chromosomes. The advantage over the *ph1* mutant method is that there is no need for aneuploids such as the N5B-stock.

1.12.5. Shortening of an alien segment

The reduction of the alien chromatin surrounding a transferred gene is a precaution against the possible introduction of deleterious genes with a desirable gene.

A reduction in the length of the alien segment introduced during wheat-alien translocation, and an improvement in the precision of a wheat-alien transfer, can be attained by the production and use of an alien telosome for the arm carrying the desired gene instead of a complete alien chromosome (Sears, 1981). To obtain an alien telosome may not be difficult since the complete

chromosomes when monosomic tend to misdivide at a relatively high rate, giving rise to telosomes.

Shortening of a transferred alien segment can be achieved by allowing recombination between two transfer chromosomes (Fig. 11) (Sears, 1972, 1981, 1983). One of the chromosomes should have its exchange point proximal to the targeted alien gene and the other distal. These two chromosomes will be homologous only in the segment of alien chromatin they have in common (including the gene in question). Any recombination occurring in this region should produce a wheat chromosome with an intercalated alien segment.

Another way of shortening an alien segment in a transfer chromosome is by inducing it to pair with a corresponding portion of its wheat homoeologue (Fig. 12) (Sears, 1981, 1983). This can be done by combining a transfer chromosome with its corresponding wheat homologue in a plant with a genotype that promotes homoeologous pairing (*phph* or Ph^{I-}). If homoeologous recombination occurs between the corresponding alien and wheat segments, part of the alien segment will be replaced with wheat chromatin resulting in a shorter alien segment.

1.12.6. Wheat-alien translocations induced by irradiation

Between the 1940s and 1960s ionizing radiation was been employed as a last resort in attempts to induce wheat-alien translocations (Sears, 1981). In this way resistance to leaf rust and stem rust was transfered from *Triticum*, *Thinopyrum* and *Secale* species (Sears, 1956; Knott 1978; 1989b; Feldman, 1988). However, this method has serious disadvantages. Ionizing radiation breaks chromosomes at random and often causes random exchanges that result in genetic imbalance (Jiang et al., 1994). Translocation frequently occurs between the alien chromosome and non-homoeologous wheat chromosomes resulting in deficiencies for a wheat segment and a duplication of genes carried by the alien segment (Feldman & Sears, 1981). For a translocation to be agronomically useful it should always involve the replacement of a homoeologous region on a wheat chromosome (Sears, 1972; Feldman & Sears, 1981). This means that the chance of obtaining an acceptable transfer by radiation is small and its verification requires extensive cytological work.

At present ionizing radiation is employed where alien gene transfer can not be achieved through the induction of homoeologous pairing. Such transfers will involve less closely related *Triticum* (formerly *Aegilops*) species from the secondary gene pool (containing the M-, U- and N-genomes) and the distantly related species from the tertiary gene pool (e.g. the genera *Agropyron*, *Elymus*, *Secale* etc.) where there is very little homoeology with the wheat genomes (A, B, D).

1.12.7. Wheat-alien translocations induced by tissue culture

There are indications that passage through a cell culture induces chromosome translocations in intergeneric or interspecific hybrid plant tissues (Larkin & Scowcroft, 1981). This has the potential to facilitate alien gene transfer between very distantly related species. Various workers observed increased multivalent formation and homoeologous pairing in tissue culture regenerated plants (for review see Feldman, 1988). Variations in the derivatives of such plants, most

probably the result of chromosome exchanges, were also observed. Although the cause of somaclonal variation and the mechanism of chromosomal translocation in callus cultures is not yet known, there are indications that the period of culture prior to regeneration, and the culture conditions, determine the manner and the degree of chromosome reorganization (Feldman, 1988; Jiang et al., 1994). Furthermore, results of cytological analyses suggest the involvement of non-homoeologous chromosomes in the translocations. Therefore, problems similar to those associated with ionizing radiation can be expected. Nevertheless, this method is a workable means for the induction of wheat-alien chromosome translocations.

1.12.8. Translocations induced by gametocidal genes

Gametocidal (*Gc*) genes derive from different *Triticum* (formerly *Aegilops*) species. Thus far, they have been reported in the former *Aegilops* sections Polyeides (*T. triunciale, T. dichasians, T. cylindricum*) and Sitopsis (*T. longissimum, T. sharonense, T. speltoides*) (Endo, 1978, 1990; Tsujimoto & Noda, 1988). The gametocidal genes derive their name from the fact that their presence in the heterozygous condition causes the abortion of gametes not carrying them (Endo, 1978). Some of the gametocidal chromosomes can cause random chromosome breakage and exchange resulting in chromosomal aberrations (reviewed by Endo, 1990; Feldman, 1988). Feldman & Strauss, (1983) reported a "genome restructuring" gene in *T. longissimum* that causes a wide range of chromosomal aberrations, including translocations, in the hybrid F_1s of crosses with wheat, as well as in the derived amphiploid. Generally, when gametocidal genes with such mutagenic action are introduced into wheat-alien addition or substitution lines, random chromosome translocations can be expected in the derived selfed generations (Endo, 1988, 1990). Tsujimoto & Noda, (1988) found a suppressor gene of the gametocidal gene in *T. triunciale* in the common wheat cultivar Norin 26. In the presence of the suppressor, plants heterozygous for the gametocidal gene, can produce progeny that lacks *Gc*. The latter progeny then includes a high proportion of plants with rearranged chromosomes. This system may therefore also be exploited to obtain wheat-alien translocations in wide crosses.

1.13. Very wide hybridization

Lately, considerable effort has been put into the improvement of techniques and has greatly extended the range of wide hybridization experiments (Mujeeb-Kazi & Kimber, 1985; Jiang et al., 1994). At present, crosses of wheat with hundreds of species in the Triticeae (*Hordeum, Agropyron, Elymus, Secale, Hayanaldia* etc.) and beyond (maize, sorghum, pearl millet) appear possible (Jiang et al., 1994; Mujeeb-Kazi & Wang, 1995; Mujeeb-Kazi 1995). Extensive selection for host and donor genotypes often helps to overcome some of the post-hybridization barriers such as chromosome elimination, hybrid sterility, adverse genetic interactions leading to hybrid dysgenesis, preferential transmission of certain alien chromosomes. (Jiang et al., 1994). However, hybridization barriers and genetic structural differences generally limit the accessibility of the very distantly related gene pools.

A number of methods and approaches are being developed that will allow gene transfers beyond the limits to conventional wide cross methodology. These include:

- Gene transfers mediated by *Agrobacterium tumefaciens*, transposable elements and DNA viruses;
- Direct uptake of DNA by isolated protoplasts leading to stable genetic transformation;
- Microinjection of cloned DNA into microspore derived embryoids;
- Polyethylene glycol treatment and electroporation of protoplasts, particle gun bombardment, etc. (Feldman, 1988; Gustafson & Dera, 1989; Lee et al., 1990; Jiang et al., 1994).

Most of these methods require tissue culture techniques, some require the ability to regenerate plants from single protoplasts, while others are not applicable to monocots. The introduction of alien genes by the use of molecular techniques may have limitations in that the introduced genetic material may not integrate well in the wheat genotype, while the ability to induce homoeologous recombination, whenever possible, will tend to place the introduced genetic material in the best location in the wheat genome (Mujeeb-Kazi & Kimber, 19[illegible]. Nevertheless, the results from the work done so far and the difficulties experienced with the [illegible] wide hybridizations call for new solutions and the transgenic technology may well prove to be one.

1.14. Transfer of leaf rust resistance from wild species to common wheat

New biotypes of the rusts evolve continually. In order to decrease the vulnerability of the cultivated wheats to the rusts it has become necessary to diversify and broaden the genetic base for resistance among the cultivars (Zhou & Dong, 1993). In recent years increasing attention has been given to the wild relatives of common wheat as an additional source of genetic diversity for disease resistance (Kerber & Dyck, 1990). With respect to leaf rust (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*) the occurrence of resistance among the wild *Triticum* species is well documented (Table 5) (Gill et al., 1983, 1985; Frauenstein & Hammer, 1985; Raupp et al., 1988; Dhaliwal et al., 1991).

This study formed part of a long term project with the aim to identify sources of seedling resistance to *Puccinia recondita* f. sp. *tritici* in a manageable number of accessions in a wild species collection, and to initiate the introgression of the resistance to common wheat. An attempt was made to determine the following with regard to each resistant accession selected: (i) Can it be crossed successfully with hexaploid wheat (AABBDD), tetraploid wheat (AABB) or synthetic tetraploids (AADD)? (ii) Is the resistance expressed in the presence of the common wheat genomes? (iii) Is it possible to transfer the resistance loci onto wheat chromosomes?

2. MATERIALS AND METHODS

2.1. Existing wild species collection

At the onset of the study in 1992, seeds of 934 wild species accessions were available in the Department of Genetics. However, many had not been grown for many years and the seeds had low viability. Germination tests were conducted with those accessions that had been stored for medium to long periods (i.e. most of the collection). Seeds of each accession (2-3 replicates) were tested by placing 10-20 seeds on moist filter paper in Petri dishes. The percentage germination was determined after 7 days incubation at 20-22^{0}C. About 25% of the accessions tested showed good germination (>80%). One hundred and sixty three accessions (17%) did not germinate at all, even after treatment with 75 ppm gibberellic acid (GA_3). The other 540 accessions (58 % of the collection) germinated poorly and had to be renewed. During 1992-1993 all but the lost accessions were rejuvenated. By the end of 1994 a further 75 accessions (56 of them primitive hexaploid wheats and landraces) had been recovered from germplasm stored locally elsewhere. Thus, 848 accessions were available for testing from the original germplasm collection.

2.2. New germplasm introductions

A further 108 accessions were imported from countries in the Fertile Crescent and from Eastern Europe where indigenous populations of wheat relatives occur. Seeds were obtained from Israel (31 accessions representing 10 species), Syria (14 accessions representing 9 species), Bulgaria (52 accessions representing 10 species) and Yugoslavia (Serbia) (31 *T. monococcum* accessions). This expanded the collection to 956 active accessions. The countries from which the accessions of the total collection were received are listed in Table 10. The number of accessions per species are given in Table 11. The *Aegilops* and *Agropyron* synonyms under which some of the accessions were obtained are also given.

2.3. Germplasm evaluation

A total of 877 *Triticum* accessions representing 27 species and 51 accessions of the genus *Thinopyrum* (12 species) were evaluated for their seedling reaction to infection with wheat leaf rust cultures (*Puccinia recondita* Rob. ex Desm. f. sp. *tritici*). The initial evaluation was done with a mixed inoculum of five pathotypes (UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13) in order to ensure virulence to the widest possible spectrum of known *Lr* genes of wheat (Table 12). Only accessions resistant to all five pathotypes were used in subsequent crosses.

The inoculum mixture was used initially to test for resistance in the hybrids and in some of backcross progenies. Difficulties in maintaining the mixture source later led to its replacement by the highly virulent UVPrt8. After scoring infection types of progenies, plants showing the highest resistance were selected for backcrossing. Accessions which gave resistant F_1 and backcross progenies in crosses with wheat were retested with each of the 5 pathotypes individually in order to confirm the potential usefulness of the resistance found initially.

The number of plants per accession evaluated with either the inoculum mix or the individual pathotypes varied from 3 to 20 depending on the number of seeds available and on germinability. Seeds for testing were planted in sand filled polypropylene pots with volume 900 cm^2.

2.3.1. Inoculation

Prior to inoculation the spores were suspended in distilled water to which was added a few drops of a wetting agent (Tween 20 or Triton). Inoculation was done at the two leaf stage (7 to 9 days old seedlings) using either a mixture of spores or a pure culture. Leaves were atomized with the spore suspension using a sprayer with a fine nozzle. [illegible] were then covered with transparent plastic bags (210 x 300 mm) and incubated for [illegible] 18-20^{0}C. Following incubation, the seedlings were moved to a growth chamber set at temperature 22-25^{0}C and a day/night cycle 16/8h. The light intensity was approximately 7500 lux (Grolux tubes).

2.3.2. Infection type (IT) scoring

Infection type was scored according to the 0-4 scale (Roelfs et al., 1992) when the pustules were fully developed, 10-14 days after inoculation. IT score and diagnosis were as follows: 0, 0; immunity, ; and 1 resistant, 2 moderately resistant, 3 moderately susceptible and 4 to be susceptible. Symbols + and - were further used to indicate that the pustules were, respectively, larger or smaller than typical of the IT score. Three symbols were used to indicate heterogeneous reactions, viz. X to indicate a mesothetic reaction (random distribution of variable-sized uredia on a single leaf), Y to indicate that higher ITs were scored at the leaf tip, and Z to indicate that higher ITs were scored at the leaf base. The presence of excessive chlorotic or necrotic tissue was indicated with the symbols C and N respectively.

2.3.3. Spore maintenance

All pathotypes were obtained from Prof. Z.A. Pretorius, Department of Plant Pathology, U.O.F.S. and were maintained on susceptible seedlings in isolation cages to avoid contamination. At intervals of approximately 6-8 months new inoculum was acquired from Prof. Pretorius. The five pathotypes were kept separate and mixed prior to inoculation when composite inoculum was in use. For medium term storage (3 - 6 months), the spores were collected by tapping rusted plants, dried under vacuum and stored in air tight containers at ultra-low temperature (-80^{0}C). Before use, stored spores were heat shocked (37^{0}C for 10 minutes) in order to break the cold-induced dormancy and were allowed to rehydrate slowly for 2-3 hours. For short term storage, infected leaves were collected, air dried (room temperature) and stored at room temperature for up to 3 weeks. Their use did not require special procedures and they were simply suspended in water prior to inoculation.

2.4. Hybrid production

When resistance was identified in a particular accession, resistant plants were transferred to a greenhouse and crossed as the male parent with a susceptible wheat. In a number of instances the

accession included plants with different ITs. In these cases the most resistant seedlings were gr[illegible]o maturity in order to establish homozygous resistant lines. Progeny of the single plant selections were retested to ascertain their homogeneity and were then crossed as the male parents to a susceptible wheat genotype. The hexaploid wheat cultivar "Chinese Spring" (*T. aestivum* cv. Chinese Spring) was mostly used as the female parent as this cultivar possesses the *kr1*, *kr2* and *kr3* genes (Falk & Kasha, 1983) for interspecific crossability. Other advantages of Chinese Spring are high susceptibility to leaf rust in the seedling stage, the availability of a complete aneuploid series that can later on be used for gene mapping, and the fact that it is the reference genotype for genetic studies in wheat.

2.4.1. Bridging species

Two accessions of *T. turgidum* ssp. *persicum* v. Stramineum (No. 293 TuPeS, and No. 294 TuPeS, received from I. Ohtsuka, Kihara Institute for Biological Research, Japan) were used as bridging parents to facilitate crosses where the ploidy differences in parents proved to be an obstacle to hybridization. The two *persicum* accessions were chosen because of their reported ability to induce spontaneous autoduplication in the F_1 hybrid (Xu and Dong, 1992). Two allotetraploids, obtained from the late Prof. E.R. Sears, Dept. of Agronomy, U.M.C., USA, and genomically AADD (A2773 = *T. monococcum* ssp. *boeoticum* X *T. tauschii* P83-66.1-1 and A2826 = *T. monococcum* X *T. tauschii*) were also used as bridging parents in some crosses.

All the wheat parents used were susceptible to the leaf rust pathotypes used in the seedling stage. CS is known to possess the leaf rust resistance genes *Lr12*, *Lr34* and *Lr31* (Dyck, 1991).

2.4.2. Growth promoting agents and embryo rescue

Crosses that were unsuccessful in the first attempt were repeated using growth promoting agents and/or embryo culture. Growth promoting agents such as the auxins 2,4-D (2,4-dichlorophenoxyacetic acid) (Kruse, 1974; Laurie & Reymondie, 1991) and Dicamba (3,6-dichloro-2-methoxybenzoic acid) (Papenfuss & Carman, 1987; R. de V. Pienaar, 1993 - personal communication) as well as the hormone GA_3 (gibberellic acid) (Larter & Chaubey, 1965; Sharma & Gill, 1983) were used for this purpose. The chemicals were applied at various concentrations (2,4-D at 10, 20 or 50 mg l^{-1} , GA_3 at 75, 100 or 150 mg l^{-1}, Dicamba at 10, 20 or 50 mg l^{-1}) 24 to 48 h post-pollination by injecting an aqueous solution into the last internode of the tiller. This was followed by the application of a few drops of the solution in each floret or by spraying the whole plant.

Embryo rescue was performed at 18-22 days post-pollination. The embryos were excised under sterile conditions and cultured on Difco Orchid agar medium (27.5 g l^{-1} supplemented with 8 g l^{-1} sucrose according to Laurie & Bennett, 1988) in Petri dishes. The Petri dishes were incubated at 24^{0}C with a 16h photoperiod (Grolux tubes). As soon as the roots and shoot developed the plantlets were transferred to pots where further development took place. Embryo rescue was restricted to cases where endosperm degeneration was observed.

2.4.3. Pollination

Crosses were made using plants grown in a greenhouse. Florets on immature spikes were emasculated and covered with glycine bags. A few days later the florets were cut open, pollinated with pollen of a wild species and covered again. Mature anthers that were about to shed pollen were collected for pollination. Initially the pollen was deposited onto the stigmas, using forceps to empty the anther contents over the cut floret. Later on, a small brush was used to collect and apply the pollen grains. In a few instances pollination was easier to achieve if the emasculated florets were cut open and bagged for 3-4 days together with a flowering spike of the male parent. The pollen shedding ear was positioned 10-15 cm higher than the emasculated ear and shaken a few times per day in order to assist the release of pollen grains from the anthers. The latter method was applied in an attempt to overcome fertility problems in the F_1 hybrid and to facilitate the production of B generations. The method was used extensively in the production of B generations as the recurrent parent, CS, was a good pollen provider. This ensured that a stigma was exposed to freshly shed pollen over a long period of time.

2.4.4. Seed dormancy

F_1 and B_nF_n seeds were temperature treated prior to planting by exposing them repeatedly (3-5 times) to low (4^0C) and high temperatures (37^0C) for periods of up to 48h. This successfully broke seed dormancy and resulted in good germination.

2.5. Verification of hybridogenic origin

In order to verify the F_1 hybrids, root tip chromosome counts were made in instances where the parents had different chromosome numbers. The mitotic chromosome numbers of the hybrid F_1s were determined from squashes of root-tip cells using the Feulgen staining technique. Two to five root tips per plant and at least five cells per root tip were analyzed. Phenotypic verification was possible with most of the hybrids as they showed a phenotype distinctly different from the female parent. Most hybrids were also completely male sterile (excluding some of the *T. turgidum* hybrids) and also showed high levels of female sterility. Phenotypic verification was especially helpful when the interspecific hybrids had parents with the same chromosome numbers.

2.6. Amphiploid production

All hybrids derived from crosses between CS and diploid or tetraploid species were treated with the antimitotic agent, colchicine, in order to produce amphiploids and to ensure fertility in the F_1 during backcrossing. In most cases the base and roots of the F_1 seedlings were immersed in an aqueous solution of colchicine with a concentration of 0.15%, 0.1%, 0.075% or 0.05%. The time of exposure varied between 7 and 24h (7, 8, 10, 15, or 24 h). Concentrations and times of treatment were varied depending on previous experience with the specific cross combination. After treatment the roots were washed thoroughly and the treated plants were placed in constantly airated water, covering the roots, for 72 h in the dark at 4^0C.

Alternative procedures of colchicine treatment were also tried in instances where doubling proved to be difficult as follows:

1. Mature embryos were excised aseptically from sterilized soaked (24h) seeds and placed for 24h or 48h on Difco Orchid agar medium (27.5 g l^{-1} supplemented with 8 g l^{-1} sucrose according to Laurie & Bennett, 1988) to which a filter-sterilized colchicine solution (concentration 0.1%, 0.05% or 0.01%) was added.
2. Sterilized seeds were germinated and the germinating embryos were aseptically transferred for 24h or 48h to Orchid medium to which filter-sterilized colchicine solution with a concentration of 0.1, 0.05 or 0.01 percent was added.
3. Dry or germinating seeds were placed on the surface of a sand layer in a Petri dish. The sand was wetted with a colchicine solution (concentration 0.1 or 0.05%) and the seeds were allowed to germinate and grow for 24h or 48h.

2.7. Production of backcross progeny

The F_1 hybrids (both colchicine treated and untreated) were backcrossed using CS as the recurrent male parent. Thus, the functional female gametes were fertilized by balanced ABD gametes from CS. Generally, backcrossing is expected to improve fertility sooner than self-fertilization. Following each backcross, resistant BF_1 plants were identified for further backcrossing.

3. RESULTS

3.1. The genus *Triticum*

All accessions of the following species were susceptible to the inoculum mix (UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13): *T. aestivum* (AABBDD, primitive wheats and land races), *T. bicorne* (S^bS^b), *T. comosum* (MM), *T. juvenale* (DDMMUU), *T. uniaristatum* (NN), *T. urartu* (AA) and *T. ventricosum* (DDNN) (Table 13). These were therefore not used in crosses with CS. Among the accessions of the remaining species of the collection resistant accessions were found and utilized as follows:

***T. columnaris* (UUMM):** The four accessions tested with the inoculum mix were all resistant and their ITs ranged from ; to 1+ (Table 14). All were crossed successfully to CS. The resultant F_1s produced slightly less resistant ITs than the respective species parents (Table 15). The hybrid F_1s 3-A-017, 3-A-058 and 3-A-066 (Table 14) were resistant to the inoculum mix as well as to pathotype UVPrt8. The fourth hybrid (3-A-025) proved to be moderately susceptible to UVPrt8 and it was therefore excluded from the study. Numerous attempts to double the chromosome numbers of the resistant F_1s through colchicine treatment eventually resulted in segmental self-fertility in 3-A-058 and 3-A-066. The B_1F_1: 3-A-058/CS produced on the doubled F_1 was self-fertile and allowed for the production of a B_1F_2. All the B_1F_2 plants tested were resistant (IT ;-1=) and were backcrossed to CS. However, no further backcrosses were made since an alternative attempt to backcross the primary allohaploid F_1 to the CS parent was also successful and had already progressed to the B_3F_1: 3-A-058/*3 CS. In the second cross (3-A-066) plants with segmental seed set were eventually produced. However, at this stage a B_2F_1: 3-A-066/*2 CS was already produced following pollination of the allohaploid F_1. The B_3F_1: 3-A-066/*3 CS was not self-fertile. In cross 3-A-017 the F_1s were generally sterile having complete male sterility but only partial female sterility which allowed B_1F_1: 3-A-017/CS seeds to be produced. Four subsequent generations of backcrossing restored a large degree of self-fertility.

High levels of resistance were detected among the plants produced by the final backcrosses, i.e B_3F_1: 3-A-066/*3 CS (IT ;), B_3F_1: 3-A-058/*3 CS (IT ;-1-), and B_4F_1: 3-A-017/*4 CS (IT ;) (Table 14). B_4F_2: 3-A-017/*4 CS and B_3F_2: 3-A-058/*3 CS were produced which will form the basis for further backcrossing. The chromosome numbers of the plants with the lowest ITs in the three crosses were determined and were as follows: B_3F_1: 3-A-066/*3 CS $2n = 48$, B_3F_1: 3-A-058/*3 CS $2n = 45$ and B_4F_1: 3-A-017/*4 CS $2n = 40$.

***T. crassum* (DcDcXX or D-DcXXDD):** Twenty three accessions, 17 of which were new introductions, were tested for resistance. Two were found to be moderately resistant (137-CR 6x with IT ;1=-2+ and 840-CR 4x, IT 1-2+), eight moderately susceptible (ITs from 2++ - 3) and 12 susceptible. The two moderately resistant accessions were crossed successfully with CS and the hybrid F_1s were tested with UVPrt8. All F_1 seedlings tested in both crosses produced moderately susceptible to susceptible reactions (IT 3 and IT 4). When the wild parent of each hybrid was also tested with UVPrt8, moderately susceptible infection types similar to those of the

respective hybrid F_1s (IT 3), were obtained. None of the hybrids was therefore used in further backcrosses.

***T. cylindricum* (CCDD):** Of the 15 accessions evaluated, two (183-CY and 590-CY) were found to be highly resistant, one moderately resistant to moderately susceptible (744-CY IT ;2^{++}), and 12 susceptible (Tables 13, 14). Hybrids were produced following the pollination of CS with the highly resistant entry 590-CY (cross 3-A-059). Accession 183-CY appeared to segregate for resistance and was therefore self-pollinated beforehand for two generations. A plant with IT ;N was isolated from the selfed progeny and was crossed as the male parent with Chinese Spring (cross 4-A-064). When the F_1: 3-A-059 was tested with the inoculum mix, lower levels of resistance, as compared to the parental species, were observed. Whereas 590-CY produced an IT = ; with UVPrt8, the F_1: 3-A-059 developed an IT = 1-2. A lower level of resistance also occurred in the F_1 produced from 4-A-064. The parent, 183-CY was resistant (IT ;) when tested with UVPrt8 while the F_1: 4-A-064 had an IT of ;-1^+. The moderately resistant accession (744-CY) was also crossed with CS. However, the F_1s developed moderately susceptible reaction types (3C) to UVPrt8 and the cross was not pursued any further. The resistant hybrid F_1s produced in crosses 3-A-059 and 4-A-064 were treated with colchicine. Segmental self-fertility was induced only in the 3-A-059 F_1s. The fertility of the hybrids improved slightly after the first backcross. In the B_2F_1: 3-A-059/*2 CS, seedlings that were resistant or moderately resistant to UVPrt8 were isolated for use in the next backcross (B_3). The colchicine treatment of the F_1: 4-A-064 is being continued.

***T. dichasians* (CC):** Two accessions were found to be highly resistant (741-DI & 742-DI, both with IT = ;) and four susceptible (Table 13). One of the resistant accessions (741-DI) was crossed successfully to CS and viable F_1 plants were produced. Upon inoculation with UVPrt8 the F_1 showed a susceptible IT although the wild parent was highly resistant (IT ;) to the same pathotype. Accession 742-DI did not flower in the greenhouse environment during the winter season of 1993. When planted again during the summer it did flower but the anthers were shrivelled and necrotic. This cross could therefore not be made.

***T. kotschyi* (UUSS):** Three of the accessions tested were found to be resistant, two moderately susceptible and two susceptible (Table 13). The three resistant accessions were crossed successfully to CS. In cross 3-A-051, some of the F_1 plants were derived through embryo rescue. The respective F_1s were tested for resistance. The F_1: 3-A-051 was inoculated with the inoculum mix and the other two F_1s (4-A-032 and 4-A-096) were inoculated with UVPrt8. There was no decrease in the level of resistance expressed in the F_1s compared with the resistance observed in their corresponding wild parents (Tables 14, 15). All the hybrid F_1s were treated with colchicine. Self-fertility occurred in the F_1: 3-A-051 and it produced segmental seed set. Self-fertility persisted and improved in subsequent backcross generations. The F_1s of the other two hybrids, 4-A-032 and 4-A-096, did not respond to colchicine treatment and no selfed seed was obtained. Nevertheless, partial female fertility of the hybrids made possible the production of a B_1F_1: 4-A-032/CS. Resistant B_1F_1 plants were identified (Table 14). No B_1F_1 seeds could be obtained from the F_1: 4-A-096, although repeated attempts at backcrossing were made. Backcrossing has

progressed well with the 3-A-051 source and B_3F_1 and B_3F_2 were produced. All the B_3F_1: 3-A-051/*3 CS seedlings tested proved to be resistant to UVPrt8 (IT ;-1=). Root tip chromosome counts of the most resistant B_3F_1 plant showed that it had a chromosome number of $2n = 44$.

***T. longissimum* (SS):** Eighteen accessions were tested with the inoculum mix of five pathotypes. Eight proved to be resistant (ITs ranging from ; to ;1+), two moderately resistant (ITs ;1+-2 and IT ;2-) and eight moderately susceptible to susceptible. Direct crosses of the resistant entries with CS were attempted and proved to be difficult. After numerous attempts at direct hybridization with CS, crosses involving the two resistant accessions, 483-LO (IT ;1-) and 142-LO (IT ;), produced only a number of inviable hybrid seeds. The resistant entries was therefore also crossed with a susceptible *T. turgidum* ssp. *persicum* v. Stramineum accession (293-TU) in attempt to construct a bridge genotype that would facilitate introgression. Crosses of the resistant accessions 142-LO and 169-LO (IT ;) as well as the moderately resistant accession 878-LO (IT 2+) with 293-TU yielded a few F_1 hybrid seeds. Upon inoculation with UVPrt8, the hybrid F_1s from the three cross combinations produced moderately susceptible infection types. As the resistance appeared to be suppressed by the wheat genomes, no further transfer attempts were made.

An amphiploid (84-S-339) was produced by prof. R. de V. Pienaar (1993, personal communication) that has the pedigree: *T. longissimum* (483-LO)/*T. monococcum* v. Sinskaje (972-MO). 84-S-339 was resistant to the inoculum mix and was later used in reciprocal crosses with CS. F_1 hybrid seeds were produced in both directions, but the seeds obtained from cross 4-A-113, (in which CS was used as the female parent) were shrivelled inviable. The F_1 seeds from the reciprocal cross (4-A-115, in which CS was used as the male parent) were viable. When inoculated with UVPrt8 the F_1: 4-A-115 produced a mixed infection type of resistance at the tip of the leaf and susceptibility at the base of the leaf (IT ;C-4Z).

***T. machrochaetum* (UUMM):** Seventeen accessions occur in the collection, 12 of which are new introductions. Seven accessions were found to be immune (IT = 0), three highly resistant (;1=), one moderately susceptible (IT 2++-3) and six susceptible. Three of the 10 resistant accessions either failed to flower under our greenhouse conditions and remained in the vegetative stage, or they produced shrivelled anthers containing little or no pollen. These accessions could therefore not be crossed to CS. Another two accessions (767-MAC and 768-MAC) were crossed to CS. In both crosses F_1 plants were obtained by means of embryo rescue. Upon inoculation with the inoculum mix, the F_1: CS/767-MAC proved to be immune (IT 0;) and the F_1: CS/768-MAC was highly resistant (IT ;). These plants later died in the greenhouse shortly after being treated with colchicine, and after two accidental, consecutive sprays with pesticides. On the second attempt, F_1s were produced only with 4-A-159 (CS/768-MAC). The remaining five accessions were crossed successfully to CS. All crosses produced hybrid F_1 seeds, yet those derived from the cross CS/769-MAC were embryoless. Some of the F_1 plants involving accession 3-A-023 were obtained through embryo culture. All the F_1 plants tested from these crosses were resistant (Table 14). The F_1s of plant 3-A-023 were tested with the inoculum mix and no decrease in the expression of the resistance was observed. The F_1s of the other four crosses were tested

with UVPrt8 alone. A slight decrease of resistance was observed (Tables 14, 15). All the resistant F_1 hybrids were colchicine treated. The colchicine treated plants of four crosses (4-A-162, 4-A-150, 4-A-151 and 4-A-159) are being grown in a greenhouse. Chromosome doubling could not be achieved with the fifth hybrid (3-A-023). The F_1: 3-A-023 was, however, successfully backcrossed for four generations. In the B_4F_1: 3-A-023/*4 CS moderately resistant plants with IT X were recovered. Self-fertility appeared after two backcross generations and improved continuously. A B_4F_2 was produced which will form the basis for further backcrossing. At the same time further B_4F_1 plants were produced some of which had lower ITs (; and ;-1=). The chromosome number of the resistant B_4F_1 plants with IT ; was $2n = 47$.

***T. monococcum* (AA):** Of the 88 accessions tested 30 were found to be resistant, 11 moderately resistant, nine moderately susceptible and 38 susceptible (Table 13). Five of the resistant accessions (three *T. monococcum* ssp. *boeoticum* and two *T. monococcum*) were successfully crossed to different parents and hybrid F_1 plants were recovered. The three *T. monococcum* ssp. *boeoticum* accessions (501-MO, 724-MO and 725-MO) were crossed successfully to CS. The small number of hybrid F_1 plants obtained in all three crosses were recovered by means of embryo rescue. Generally, the plants were very weak and in one of the crosses (CS/501-MO) the plants were so poorly developed they could not be tested. In the other two crosses the F_1 plants were all susceptible to the inoculum mix. One of the *T. monococcum* accessions was an autotetraploid derived from 12-MO. Upon crossing it to CS one hybrid seed was produced which proved to be susceptible to the inoculum mix.

The other *T. monococcum* accession, 972-MO (IT ;N), was crossed as the male parent to (a) CS, (b) two allotetraploids, obtained from the late Prof. E.R. Sears, Dept. of Agronomy, U.M.C., USA, and genomically AADD (A2773 = *T. monococcum* ssp. *boeoticum* X *T. tauschii* P83-66.1-1 and A2826 = *T. monococcum* X *T. tauschii*) and (c) *T. monococcum* ssp. *persicum* v. Stramineum (293-TU). All accessions used as female parents were susceptible at the seedling stage to the rust pathotypes used. The crosses were made in a attempt to establish whether or not the resistance derived from 972-MO is expressed in the presence of the genomes of the female parents (AABBDD, AADD and AABB).

Hybrid F_1 seeds were produced in all four combinations, although the combination with A2826 (4-A-105) produced only inviable seeds. The F_1s of the three successful crosses were inoculated with UVPrt8. The F_1 plants from cross 4-A-068 (A2773/972-MO) and 4-A-070 (CS/972-MO) were susceptible, while the F_1s from the cross 4-A-069 (293-TU/772-MO) were resistant (IT 1+CN). The resistant F_1s were pollinated with CS. Two F_1 seeds were produced in the cross 4-A-154 (293-TU/772-MO//CS). When inoculated with UVPrt8 both were susceptible. As it appeared that the *T. monococcum* resistance genes are often suppressed in hybrids with wheat, no further hybridizations with this species were attempted.

***T. ovatum* (UUMM):** Seventeen accessions were tested (including 11 new introductions). Eight accessions were found to be resistant, five moderately resistant and only four susceptible (ITs 2++ to 4). The eight resistant accessions and four of the moderately resistant accessions were crossed successfully to CS. Hybrid F_1s were produced with 10 accessions including two that

were moderately resistant. Two of the crosses had to be repeated due to poor viability of the F_1. Upon inoculation with UVPrt8, hybrid F_1s in five of the crosses, (three from resistant and two from moderately resistant species parents), developed susceptible infection types. Two of the above mentioned hybrid F_1s were also tested with the inoculum mix and were confirmed to be susceptible. Nevertheless, six hybrid F_1 combinations, 3-A-097, 4-A-063, 4-A-112, 4-A-138, 4-A-139 and 4-A-143, expressed resistance (Table 14). The F_1: 3-A-097 was also tested with the inoculum mix and showed moderate resistance. Plants from all the resistant hybrid F_1s were treated with colchicine. The F_1: 3-A-097 produced doubled segments that were self-fertile and gave a low seed set. During subsequent backcrossing to CS, the self fertility of the hybrid progeny improved. The colchicine treated F_1s of the remaining five crosses are being grown in a greenhouse. The F_1: 3-A-097 was backcrossed three times to CS and a B_3F_1: 3-A-097/*3 CS was obtained. In the B_3F_1: 3-A-097/*3 CS, plants with ITs ;-1= and X were identified. A chromosome count of the IT ;-1= plant revealed that it had $2n = 53$ chromosomes.

***T. peregrinum* (UUSS):** With the exception of two accessions, one moderately susceptible and one susceptible, all others (eight accessions) were found to be resistant to the inoculum mix (Table 13). Seven of those were successfully crossed to CS. All the F_1 hybrids expressed resistance (Table 14). The F_1s of two of the crosses were tested with the inoculum mix, four were tested with UVPrt8 and one was tested with both. The hybrid 3-A-044 produced a more resistant infection type (IT ;N) when tested with the inoculum mix than did its wild parent, 488-PE (IT ;1-) (Tables 14, 15). Due to difficulty in producing B_1F_1s from F_1 restitution nuclei, numerous colchicine treatments were also attempted. Low segmental seed set was obtained in the colchicine treated hybrid F_1s: 3-A-044, 4-A-021 and 4-A-023, although these seeds were eventually not used to produce of B_1F_1s. Following numerous attempts all but one hybrid (4-A-087) produced B_1F_1 seeds from restitution nuclei. Up to now B_1F_1s have been produced from the F_1s: 4-A-021, 4-A-023 and 4-A-090, B_3F_1s and B_3F_2s from: 3-A-044 and 3-A-016 and B_4F_1s, as well as a few B_3F_2 seeds, 3-A-016 from. Plants with high levels of resistance were identified in all the backcross generations of all crosses (Table 14). Chromosome counts on the most resistant plants among the B_3F_1s and B_4F_1s showed a chromosome number of $2n = 44$ in the B_3F_1: 3-A-065/*3 CS, mixoploidy in the B_3F_1: 3-A-044/*3 CS (with chromosome numbers ranging from $2n = 42$ to $2n = 49$), and $2n = 43$ in the B_4F_1: 3-A-016/*4 CS.

***T. searsii* (S^sS^s):** The collection includes 32 accessions of which 29 are recent introductions. Ten accessions were found to be resistant, two moderately resistant, two moderately susceptible and 18 susceptible (Table 13). Slow development of the plants (9-14 months), a tendency to remain vegetative under local climatic conditions, poor anther development and high sterility hampered attempts to hybridize the resistant accessions, especially the new introductions, with CS. Numerous attempts were made to produce hybrid F_1 seeds in the resistant accessions. Almost all attempts failed when CS was used as a parent. The only exception, cross combination CS/145-OV, produced highly shrivelled and inviable seeds. Generally, the first signs of seed degeneration were visible as early as 11-13 days after pollination. Embryo rescue was attempted but with no success. A cross of accession 814-SE with the tetraploid 293-TU (*T. turgidum* ssp. *persicum* v.

Stramineum) resulted in the production of hybrid F_1 seeds. However, the F_1s were susceptible to UVPrt8 and no backcrossing was attempted.

T. sharonense **(S^{l}S^l):** Thirteen plants occur in the collection, four of which were found to be resistant, three moderately susceptible and six susceptible (Table 13). Three of the resistant accessions were successfully crossed to CS and hybrid F_1 seeds were obtained. The resistance of two of the accessions, 148-SH and 174-SH, was retained in their respective hybrid F_1s, 3-A-010 and 4-A-025 (Tables 16, 17). The F_1: 3-A-010 was tested with the inoculum mix while 3-A-010 was tested with UVPrt8. The third accession, 587-SH (IT ;1=), produced moderately susceptible F_1 hybrid seedlings (IT 3) when tested with the inoculum mix, and a susceptible infection type when tested with UVPrt8. It was therefore not used in further backcrosses. The resistant hybrid F_1 plants from crosses 3-A-010 and 4-A-025 were colchicine treated. Self-fertility was observed in both hybrids. In 3-A-010, the self-fertility was low and sporadic, while in 4-A-025 many seeds were formed. Resistant plants were selected among the selfed progeny of cross 3-A-010. Four backcrosses of the 3-A-010 resistance resulted in B_4F_1: 3-A-010/*4 CS plants with high levels of resistance (ITs 0; and ;-1=) and a chromosome number of $2n = 46$. A B_4F_2 was produced and will form the basis for further backcrosses. Following backcrosses with the 4-A-025 source, B_2F_1: 4-A-025/*2 CS seeds were produced. Self-fertility in this cross was good and improved with almost 100% after only one backcross. In the B_2F_1: 4-A-025/*2 CS plants with a moderate level of resistance (IT ;-2Z) were identified.

T. speltoides **(SS):** Seven of the 11 accessions were found to be resistant, one moderately resistant and three moderately susceptible (Table 13). Five of the seven resistant accessions were successfully crossed to CS. Of the two remaining resistant accessions, one (739-SP) was sterile and the other (140-SP) did not flower in the greenhouse environment utilized. Four of the fertile, resistant accessions (150-SP, 681-SP, 691-SP and 692-SP) produced viable F_1 seeds in crosses with CS while the fifth (151-SP) failed to do so. The tested F_1s from the viable hybrids were all resistant to infection with UVPrt8. Two of the hybrid F_1s, 3-A-012 and 3-A-013, were also tested for their reactions to the inoculum mix and were found to be resistant. Resistance in accession 150-SP has already been transferred to wheat (Marais & Pretorius, 1995) and the hybrid involving this parent was therefore not backcrossed to CS. The remaining resistant hybrid F_1s were treated with colchicine. Low self-fertility from segmental chromosome doubling was observed in the F_1s: 3-A-012 and 3-A-013. The third hybrid (4-A-137) was colchicine treated and the plants are being grown in a greenhouse. The resistant F_1s: 3-A-012 and 3-A-013, were successfully backcrossed to CS for several generations. With the exception of the last backcrosses, which were done under unfavourable greenhouse conditions (low light intensity, high humidity) during the winter, the levels of self-fertility of the BF_1s improved with progressive backcrossing. From the hybrid 3-A-012, B_4F_1: 3-A-012/*4 CS seeds were derived from which plants with a high level of resistance were selected (IT 0;) (Table 14). B_4F_2 seeds were also obtained. Following backcrossing of the F_1: 3-A-013, B_5F_1: 3-A-013/*4 CS and B_5F_2 seeds were produced. Among the B_5F_1: 3-A-013/*4 CS plants tested with UVPrt8, high levels of

resistance (IT ;) were also detected. Resistant plants with chromosome numbers of $2n = 44$ in the B_4F_1: 3-A-012/*4 CS and $2n = 43$ in the B_5F_1: 3-A-013/*4 CS were identified.

***T. syriacum* ($C^cC^cXXS^sS^s$):** Thirty four accessions, 33 of them being newly introduced, were tested for resistance. Nine were found to be resistant, six moderately resistant, 14 moderately susceptible and five susceptible (Table 13). Most accessions grew poorly under the greenhouse conditions. They developed slowly (9-14 months) and formed poorly developed flowers which produced shrivelled anthers and were generally sterile. Since only small amounts of pollen were available, hybridization with this species proved to be difficult. Four accessions, of which only one (849-SY) showed a satisfactory level of resistance (Table 14) were crossed successfully to CS. Three of the four hybrid F_1s were susceptible to UVPrt8. This was not unexpected in view of the ITs they produced following infection with the inoculum mix, i.e. 852-SY produced IT ;-2$^-$ and ;-4, 854-SY produced ITs ;-;2$^-$ and 876-SY produced ITs 1^{++}-3^+. The fourth hybrid (4-A-022) was resistant (IT ;-1$^=$), but the F_1 plants lacked vigour and could not be tested in the seedling stage. Some of the resistant F_1 plants were treated with colchicine although only a low frequency of chromosome doubling was expected to occur due to the high ploidy levels of the two parents. No self-fertility was observed among the colchicine treated plants. The hybrid could, however, be backcrossed to CS and B_1F_1: 4-A-022/*1 CS plants that were resistant to UVPrt8 could be identified (Table 14).

***T. tauschii* (DD):** Thirty accessions were tested. Two proved to be resistant, two moderately resistant, four moderately susceptible and 22 susceptible (Table 13). Several attempts to hybridize the two resistant accessions with CS were not successful. No hybrid F_1s were produced from the highly resistant 674-TA (IT 0;). After a number of hybridization attempts with 529-TA (IT ;-1$^=$) one seed was produced. The embryo was rescued after 18 days, but the plant which developed from it died shortly after inoculation.

***T. timopheevii* ($A^mA^mA^nA^nGG$):** Seventy two accessions were tested with the inoculum mix. Twenty two were found to be resistant, one moderately resistant, 11 moderately susceptible and 38 susceptible (Table 13). The resistant and moderately resistant accessions were crossed to CS. The seed set was generally very good. Viable F_1 hybrid seeds were produced in all crosses. Hybrid F_1s from all 23 crosses were tested with UVPrt8 while 16 of them were also tested with the inoculum mix. Following inoculation with UVPrt8 the hybrid F_1s of 13 crosses were found to be resistant, those of six crosses were moderately resistant, those of three crosses were moderately susceptible and one F_1 was found to be susceptible. The susceptible (UVPrt8) F_1s were also found to be moderately susceptible to the inoculum mix. Five of the six F_1 combinations found to be moderately resistant to UVPrt8, were also tested with the inoculum mix. Four were resistant and one was found to be moderately susceptible (Table 14). The 13 F_1 combinations found to be resistant to UVPrt8 included two which were susceptible to the inoculum mix. The nineteen resistant hybrid F_1s were treated with colchicine and segmental self-fertility was observed in 13 of them. Complete self sterility was encountered with two of the hybrids (3-A-001 and 3-A-002), however, B_1F_1 seeds could be produced when the self-sterile colchicine treated F_1 plants were pollinated with CS. The level of difficulty encountered during

backcrossing depended on the particular accession used as the wild parent in the initial cross. Thus far, B_1F_1 plants were produced from four crosses (3-A-033/*CS, 3-A-054/*CS, 4-A-009/*CS and 4-A-065/*CS), B_2F_1 plants were produced from eight crosses (3-A-002/*2 CS, 3-A-003/*2 CS, 3-A-029/*2 CS, 3-A-030/*2 CS, 3-A-031/*2 CS, 3-A-032/*2 CS, 3-A-118/*2 CS, 4-A-002/*2 CS), B_3F_1 plants were produced from five crosses, while in three of them B_3F_2 was also produced (3-A-014/*3 CS, 3-A-022/*3 CS, 3-A-034/*3 CS, 3-A-096/*3 CS, 4-A-003/*3 CS), B_4F_1 and B_4F_2 plants were produced from one cross (3-A-005/*3 CS), and B_5F_1 and B_5F_2 plants were produced from one cross (3-A-001/*5 CS) (Table 14). With the exception of B_1F_1: 3-A-033, B_1F_1: 4-A-065 and B_3F_1: 3-A-022, in which no resistant F_1s were found, all the other backcross generation F_1s exhibited satisfactory levels of resistance. The results of chromosome counts on resistant plants from the most advanced backcross generations (B_3F_1, B_4F_1 and B_5F_1) are listed in Table 14.

***T. triaristata* (UUMM/UUMMXX):** Seven of the 11 accessions tested were found to be resistant to the inoculum mix and four were susceptible. The resistant accessions were crossed successfully to CS. High percentages of embryoless seeds were found among the F_1s derived from crosses between the female parent, CS, and three of the accessions (747-TRT, 748-TRT and 751-TRT). As a result no F_1 plants could be recovered in these crosses. Two of the crosses were repeated (CS/747-TRT and CS/748-TRT) and produced many seeds. However, most of the seeds were big but lacked an embryo. A few F_1 plants could be obtained in both crosses but proved to be susceptible to UVPrt8. F_1s from a fourth cross (CS/145-TRT) were also found to be susceptible to UVPrt8. In the remaining three crosses (3-A-100, 3-A-107 and 3-A-119) hybrid F_1s were produced. F_1: 3-A-107 was resistant to both the inoculum mix and UVPrt8, 3-A-119 was moderately resistant to the inoculum mix and 3-A-100 was resistant to immune to UVPrt8. In the last cross the resistance against UVPrt8 was expressed more strongly in the hybrid F_1s than in the respective wild parent. The resistant F_1s were subjected to a number of colchicine treatments. A low level of self-fertility was observed only in the F_1: 3-A-119. It proved very difficult to backcross the highly sterile F_1s from all three crosses. B_1F_1 progeny was produced only after spikes from F_1 plants were bagged together with flowering spikes of CS for 3-4 days. The least troublesome combination of the three, 3-A-100, was backcrossed three times. Highly resistant to immune (IT 0; and ;) B_3F_1: 3-A-100/*3 CS plants were obtained including one which had a chromosome number of $2n = 43$. However, this plant proved to be self-sterile. The F_1: 3-A-107 was also backcrossed three times to CS and resistant B_3F_1: 3-A-107/*3 CS plants were recovered. A degree of self-fertility was evident after one backcross and it further improved after the second backcross. The chromosome number of a resistant B_3F_1: 3-A-107/*3 CS plant was $2n = 56$. The F_1:3-A-119 was backcrossed once and resistant B_1F_1 plants were identified (Table 14). Although sporadic seeds were formed following backcrossing of the hybrid F_1 plants to CS, self fertility was not observed.

***T. triunciale* (UUCC):** All accessions in the collection were found to be resistant to the inoculum mix and all were crossed successfully with CS. One of the crosses (CS/773-TR) produced numerous, big, but slightly shrivelled seeds which were hollow at the site of the

embryo. No F_1s were recovered from the latter cross. F_1s from seventeen cross combinations were tested with UVPrt8. Five of them were resistant, four were moderately resistant, two were moderately susceptible and six were susceptible. F_1s from two crosses were also tested with the inoculum mix. One was found to be highly resistant to both UVPrt8 and the inoculum mix (Tables 14, 15). The expression of this resistance was stronger than the resistance of the wild parent when tested with the inoculum mix but nearly the same when tested with UVPrt8 (Tables 14, 15). The hybrid F_1s which were resistant (5 hybrids) and moderately resistant (2 hybrids) were treated with colchicine. Six were treated recently and are being grown in a greenhouse. The remaining hybrid F_1 did not produce selfed seed following colchicine treatment. However, it was backcrossed twice and in the B_2F_1: 3-A-069/*2 CS, plants with high levels of resistance were identified (Table 14).

T. turgidum **(AABB):** The 344 accessions of the collection were tested with the inoculum mix. Eighteen were found to be resistant, 10 moderately resistant, 39 moderately susceptible and 277 susceptible. The resistant and moderately resistant accessions were crossed to CS. Hybrid F_1s from 22 crosses were tested with the inoculum mix, six hybrid F_1s were tested with both UVPrt8 and the inoculum mix. The remaining six hybrids were tested with UVPrt8 only. Two of the hybrids tested with the inoculum mix were resistant, three were moderately resistant, six were moderately susceptible and 11 were susceptible. Regarding the six hybrids tested with both the inoculum mix and UVPrt8, three tested moderately susceptible with the inoculum mix and were susceptible when tested with UVPrt8. One was moderately resistant to the inoculum mix but susceptible when tested with UVPrt8 alone. Another hybrid was moderately susceptible when tested with the inoculum mix but proved to be resistant to UVPrt8. Testing with UVPrt8 alone showed two hybrids to be resistant, one to be moderately resistant and three to be susceptible (Table 14). In total eight hybrids were found to be resistant. These F_1s were treated with colchicine. All of the treated plants appeared to be self-fertile to varying degrees. Two hybrids (3-A-045 and 3-A-057) were backcrossed three times and resistant B_3F_1: 3-A-045/*3 CS and B_3F_1: 3-A-057/*3 CS plants were identified. B_3F_2: 3-A-045/*3 CS and B_3F_1: 3-A-057/*3 CS seeds were also produced. The most resistant selections produced ITs of ; and ;-1=, respectively (Table 14). Chromosome counts on these plants showed a chromosome number of $2n = 42$ in both crosses. Backcrossing with the remaining six sources progressed to the B_2F_1 (4 hybrid combinations) and the B_1F_1 (4 hybrid combinations) (Table 14). All the backcross F_1 generations were self-fertile. Four of the hybrids had close to normal self-fertility, these included three B_2F_1s (3-A-062, 4-A-004 and 4-A-008), and one B_3F_1 (3-A-057).

T. umbellulatum **(UU):** Three accessions were tested. One (740-UM) was found to be immune (Table 14, 15) and two (158-UM and 159-UM) resistant to moderately resistant (IT ;1-1++ and 2). Accession 159-UM had a low viability in the greenhouse environment and died before flowering. The other two accessions were crossed to CS. Embryo rescue was performed in both crosses, although in 3-A-104 it proved not necessary because seed set was also obtained. In both F_1 hybrids high levels of resistance to the inoculum mix were observed (3-A-104 developed a fleck and 3-A-068 = CS/159-UM developed IT ;-1-). The F_1: 3-A-104 was also tested with

UVPrt8 and produced an immune reaction (IT 0;). The F_1 of the cross: 3-A-068 (CS/159-UM) died in the greenhouse shortly after being treated with colchicine and following accidental spraying with pesticides. Attempts to repeat the cross were unsuccessful. Following colchicine treatment of the F_1: 3-A-104 two seeds were produced. A chromosome count on one of the hybrids revealed $2n = 56$ chromosomes. Sterility problems delayed the production of a B_1F_1. In order to facilitate backcrossing, F_1 ears were bagged with flowering ears of CS for several days. Eventually B_1F_1 and B_2F_1 plants were obtained. In the B_2F_1: 3-A-104/*2 CS all the tested plants were resistant to UVPrt8 (IT ;-1=) (Table 14).

All the *Triticum* accessions which produced resistant F_1 hybrids in crosses with CS were also tested with the individual rust pathotypes used in the study. The results of these tests confirmed resistance of the parents and are listed in Table 15.

3.2. Genus *Thinopyrum*

Accessions from 12 species of the genus *Thinopyrum* were tested with the inoculum mix. None of the accessions of the following species were resistant: *Th. elongatum*, *Th. caespitosum*, *Th. distichum*, *Th. scirpeum* and *Th. podperae*. In the remaining species (*Th. bessarabicum*, *Th. curvifolium*, *Th. junceiforme*, *Th. intermedium*, *Th. junceum*, *Th. turcicum* and *Th. ponticum*) nine accessions that were resistant to the inoculum mix were identified (Table 13). Eight of the resistant accessions were immune (IT 0) whereas one was highly resistant.

In view of the large number of resistant *Triticum* accessions encountered and the fact it is generally much more difficult to achieve intergeneric hybridization than intrageneric hybridization, no attempts were made to hybridize these sources with CS.

4. DISCUSSION

4.1. Evaluation of the collection for leaf rust resistance

An evaluation of 877 *Triticum* accessions representing 27 species (Tables 11 and 13) and 51 *Thinopyrum* accessions representing 12 species (Tables 11 and 13) with an inoculum mix of five leaf rust pathotypes (UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13) revealed a wealth of potentially useful resistance genes. Of the 877 *Triticum* accessions tested, 222 (25%) were found to be resistant. Of these 176 (20%) were highly resistant and the other 46 accessions (5%) were moderately resistant. The 51 *Thinopyrum* accessions tested included nine (18%) that were resistant.

Very little or no leaf rust resistance was found among the accessions of the seven *Triticum* species *T. aestivum*, *T. bicorne*, *T. comosum*, *T. juvenale*, *T. umbellulatum*, *T. uniaristatum*, *T. urartu* and *T. ventricosum*. From Table 13 it can be concluded the genome most frequently present in the susceptible species, is the D-genome (*T. aestivum*, *T. crassum* 4*x* and 6*x*, *T. juvenale* and *T. ventricosum*). Among the species that contained resistant accessions, the most regularly occurring genome was the U-genome (eight species), followed by the S-genome (six species), the C-genome (four species) and the M-genome (four species). While the associations may be purely coincidental, it may also be ascribable to the genetic distance between common wheat and the donor species.

The 222 resistant to moderately resistant *Triticum* accessions (20 species) included 42 *T. monococcum* accessions which had to be excluded from the study on the basis of frequent suppression in the hybrid F_1s of the resistance derived from the A-genome. The literature suggests that suppression of this kind occurs frequently (Kerber & Dyck, 1973). In this study suppression was observed in the F_1s of five crosses involving *T. monococcum* as the male parent. Regarding one of the accessions, 972-MO, the resistance was expressed when the accession was crossed to *T. turgidum* (AABB) but suppressed when it was crossed to either CS (AABBDD) or the allotetraploid A2773 (= *T. monococcum* ssp. *boeoticum* X *T. tauschii*, genomically AADD). Thus, the suppression of the resistance may have been due to the presence of the D-genome.

The exclusion of the 42 *T. monococcum* accessions effectively reduced the number of resistant or moderately resistant accessions that were available for hybridization from 222 to 180. Of this number, 18 resistant accessions (*T. searsii* (eight), *T. syriacum* (five), *T. macrochaetum* (four) and *T. speltoides* (one)) were not crossed to wheat at all, the reason being poor adaptability of the plants to greenhouse conditions and, as a consequence, their failure to grow, flower or to develop functional anthers. Poor adaptability was associated particularly with species introduced recently from Syria (*T. searsii*, *T. syriacum* and *T. diccoccoides*) and Bulgaria (*T. macrochaetum* and *T. speltoides*).

Of the 162 resistant accessions that remained, 10 could not be crossed to wheat despite repeated attempts. Another nine moderately resistant accessions were also not used in crosses. Upon retesting these accessions it appeared that the reactions tended towards IT 2^{++}. In view of the abundance of high levels of resistance encountered it was decided that it would not be worth

while to carry on with these accessions. Eventually, 143 accessions, representing 18 species, remained. These were crossed to CS as female parent in most cases.

4.2. Hybridization of the resistant accessions with wheat

With the exception of the diploid species, no major difficulties were encountered when crossing the resistant accessions to CS. The diploids, in particular *T. tauschii*, *T. longissimum*, and *T. searsii*, were very difficult to cross and this necessitated the use of tetraploid bridging species. While this strategy did not solve the crossability problem completely, it facilitate production of a small number of hybrids with *T. longissimum* and *T. searsii* as parents. The difficulty encountered in hybridizing the diploid species with hexaploid CS, and sometimes also with tetraploid wheat, is probably largely due to the difference in chromosome number and cross compatibility barriers which result in F_1 seed abortion and F_1 hybrid lethality (Gill & Raupp, 1987). Farooq et al. (1990) have also found that *T. tauschii* is difficult to cross with wheat even though it shares the D-genome. Consequently, successful hybrids involving the two species are rare.

In general, the seed set in most of the crosses involving the different species and accessions was relatively high and it was usually easy to produce the F_1 hybrids. However, the mature F_1 seeds from crosses of *T. longissimum* and *T. searsii* with CS and, to a lesser extent those involving *T. triaristatum* and CS, were shrivelled and often had low viability. This seemed to be the result of degeneration of the hybrid endosperm. Bai et al. (1994) have also reported endosperm degeneration in crosses of common wheat with *T. triaristatum*. These authors suggest that the development of the hybrid endosperm is affected by the genotypes of both parents. In crosses of *T. triaristatum* accessions with some durum and bread wheats, the hybrid endosperms developed normally. In the present study a similar situation may apply, not only to *T. triaristatum* but also to *T. longissimum* and *T. searsii*, which produced fairly normal seeds when crossed to a tetraploid accession of *T. turgidum* (293-TU).

Low hybrid viability was occasionally observed in crosses involving other species. *T. triuncialis* - CS hybrid seeds generally had a low germinability. In at least two cross combinations involving this species the F_1 seeds were embryoless and could not germinate. Embryoless seeds were also produced in crosses involving another two species, viz., *T. macrochaetum* and *T. ovatum*. The formation of embryoless seeds could be ascribed to the use of the growth promoting agent Dicamba in some crosses but not all.

4.3. Use of growth promoting agents

With the possible exception of Dicamba, none of the growth promoting substances appeared to improve seed set and seed quality. Treatment with Dicamba often resulted in the formation of embryoless, apomictic seeds, especially when it was applied during backcrossing of problematic allohaploid F_1s. Thus, while it did appear to improve the quality of the seeds produced it did not seem to aid in overcoming crossing barriers or problems associated with hybrid sterility.

4.4. Embryo rescue

In most cases the F_1 hybrid seeds developed fairly normally. However, in a few cross combinations it was necessary to rescue and culture the embryos. The success of embryo rescue depended on the stage of embryo development. No hybrid F_1s were recovered through embryo rescue when the embryo was excised earlier than 18 days post-pollination (e.g. CS x *T. searsii*). In the crosses: CS x *T. dichasians* and CS x *T. tauschii*, embryo rescue failed even though the embryos were excised on the 18th day post-pollination. In some instances embryo rescue was performed as a precaution or with the aim to advance more quickly to the next generation. (However, it appeared that in cases where viable F_1 seedlings could also be obtained from seeds, embryo rescue should not be used.) Plants produced through embryo culture were generally less viable and this presents difficulties in seedling tests for rust resistance.

4.5. Expression of the resistance in the hybrid F_1

The hybridization attempts produced 143 F_1 hybrids. Eight of these had very low viabilities and could not be tested for resistance to leaf rust. The remaining 135 F_1 hybrids were tested with an inoculum mix and/or UVPrt8 and could be grouped into three major categories as follows:

1. A category (indicated as E in Table 13) consisting of F_1 hybrids in which the resistance derived from the wild parent was fully expressed. Seventy six hybrids representing 15 species (Table 13) are of this type. The hybrid F_1s in the this category included some in which the level of resistance appeared to be stronger than the resistance recorded in the wild parent itself. F_1s of this type were produced by crosses of CS/*T. peregrinum* (3-A-044), CS/*T. speltoides* (3-A-013), CS/*T. timopheevii* (3-A-034 and 4-A-009), CS/*T. triaristatum* (3-A-100) and CS/*T. triuncialis* (3-A-069) (Tables 14, 15). One possible explanation for this observation is a genetic background effect resulting from interaction of Chinese Spring *Lr* gene(s) with genes for resistance in the wild species. Alternatively, the small differences in the level of resistance may have a physiological and/or environmental basis.
2. The category of hybrid F_1s (indicated as S in Table 13) in which partial or complete suppression of the resistance apparently occurs, i.e., hybrids that were moderately susceptible or susceptible although the species parent was fully resistant.
3. Hybrids deriving from species initially thought to be resistant to all the pathotypes of the inoculum mix but which in reality were incompletely resistant (indicated as NE in Table 13).

The 60 susceptible hybrid F_1s deriving from resistant and moderately resistant species parents were classified as Category 2 and Category 3 hybrids (see Table 13). Resistance in a hybrid F_1 was considered to be suppressed or partially suppressed when occurs in the seedling tests with the inoculum mix and with UVPrt8 indicated that the wild parent was resistant/moderately resistant while the F_1 was moderately susceptible to susceptible. Accessions which have been susceptible to a component or components of the inoculum mix would have produced a hybrid F_1 which lacked resistance to the specific pathotype or pathotypes. Thus, the resistance may be normally expressed yet may not be effective against all the pathotypes. Such F_1s were allocated to Category 3.

The susceptibility of hybrid F_1s could most often be attributed to suppression or partial suppression by the genome of CS (Table 13 column E). In a few cases *T. turgidum* genomes also appeared to suppress resistance genes contributed by *T. longissimum* and *T. searsii*. Resistance genes from the following species appeared to be suppressed by the common wheat genomes: *T. turgidum* (AABB) (16 accessions), *T. triunciale* (UUCC) (eight accessions) and *T. monococcum* (AA) (five accessions). When the Category 2 hybrids obtained are expressed as a percentage of the total number of crosses made with a specific species, the following results are obtained (only species in which more than five accessions were crossed, were considered): In 83% of the hybrids made with *T. monococcum* (AA) the resistance was suppressed. The resistance was also suppressed in 57% of the hybrids involving *T. turgidum* (AABB), 43% of the hybrids involving *T. triaristata* (UUMM/XX) and 38% of the hybrids involving *T. triunciale* (UUCC). Thus, it appears that F_1 suppression may be expected to occur more frequently among accessions which have the A- or AB-genomes. A mechanism that suppresses leaf rust resistance genes in common wheat, and which involves chromosomes 2D and 1D of CS, was in fact described by Bai & Knott (1991). McIntosh & Dyck (1975) showed that a gene in the cultivar Thatcher suppresses the resistance conferred by *Lr*23 to Canadian pathotypes of leaf rust and only partially suppresses its resistance to Australian pathotypes. Bai & Knott (1992) reported widespread suppression of leaf rust resistance genes in *T. dicoccoides*-common wheat hybrids. The authors speculated that the suppressors may show specificity of action and that they may be directed against a specific gene(s) for resistance. Based on their data obtained with CS x *T. turgidum* hybrids, as well as other hybrids, they claim that the presence of a general suppressor in one of the wheat genomes is unlikely. Rather, the evidence suggests that the suppression patterns show specificity. Specific patterns of suppression may also possibly be directed at genomes other than A and B. If so, this can possibly explain much of the F_1 suppression observed in this study.

In this study evidence was also found of suppression or partial suppression of resistance deriving from *T. longissimum* (142-LO and 169-LO) in crosses of *T. turgidum*/*T. longissimum*. Kerber (1983) has found evidence that the AB-genome component of tetraploid wheat is capable of inhibiting resistance conferred by the D-genome of *T. tauschii* when these genomes are combined in an amphiploid. It seems possible therefore that the A- and/or B-genome may carry suppressors that function against the S-genome as well.

Kerber (1983) states that suppression by one genomic component of rust resistance conferred by another, when these are combined into an amphiploid, is not uncommon in *Triticum*. After all, the high frequency of occurrence of suppressors in the bread wheat genomes as described in the literature suggests that they must have a selective advantage (Bai & Knott, 1991).

Another possible explanation for the occurrence of F_1 suppression among the interspecies hybrids may be intragenic interactions, i.e. dominance or recessivity of the observed resistance. Since it was not known beforehand whether the resistance gene(s) in a wild parent is dominant or recessive, it is not clear whether some of the instances of suppression in the F_1 were due to recessiveness. Hypothetically resistance might also become recessive in the hybrids if a modifying genetic system is present in the common wheat parent.

4.6. Confirmation of the resistance in the species parents

The leaf rust resistant species that also produced resistant F_1 hybrids in crosses with wheat were retested with the individual components of the inoculum mix (Table 15). The data confirmed high levels of resistance in the material. However, the results suggest that some of the accessions of a species may have contributed the same resistance genes. Thus, in order to maximize the chances of transferring diverse resistance genes, the selection of a subset of material for further manipulation should be based on infection type differences in the parents, the infection types produced by the advanced backcross segregates, and the origin of accessions.

4.7. Colchicine treatment

The optimal concentration of colchicine to apply and the duration of treatment vary depending on the genotype of the hybrid, the environmental conditions at the time of treatment, the age and physiological state of the plant. Some *T. turgidum* accessions for example produce interspecies hybrids that are capable of a high frequency of spontaneous chromosome doubling (Xu & Dong, 1992).

As a result of the difficulties encountered in most hybridizations of the wild species with wheat, too few seeds were generally produced in a specific cross to allow for proper experimentation with alternative means of colchicine application. However, the following general conclusions may be justified:

(i) There appears not to be any correlation between either the duration or dose of colchicine application and the induction of self-fertility in the treated plants. The different hybrids appeared to vary considerably regarding the time and dose required to induce chromosome doubling. Generally, plants were treated with 0.1% colchicine for 15 hours. If this proved to be ineffective, a longer treatment of up to 24 hours and/or a higher dose (0.15%) were applied.

(ii) A prolonged period of exposure to colchicine decreases the survival rate of the treated material, and unnecessarily long treatments should therefore be avoided

(iii) While the colchicine treatment does not always cause chromosome doubling, it does seem to promote seed formation when the male sterile F_1s were pollinated with CS pollen.

(iv) Colchicine treatment of mature embryos and germinating seeds appears to be more effective than the treatment of plants. All the hybrid F_1s treated in this manner showed a degree of self-fertility.

(v) Colchicine treatment of seeds is equally effective whether this is done in a sand layer or on Difco Orchid agar. However, the sand treatment is much simpler to perform.

4.8. Backcrossing and transmission of the resistance

In many instances backcrossing of the F_1 hybrid to its wheat parent was more difficult to achieve than it was to produce the hybrid F_1 itself. In some cases the production of a B_1F_1 was possible only after the florets had been cut open and bagged for 3-4 days with a pollen shedding ear of the recurrent parent. Evidently, the procedure exposed the stigma to freshly shed pollen over a longer period of time. As a result, functional pollen was available at a time of peak receptivity of the stigma.

Generally, producing the B_1F_1 and sometimes the B_2F_1 as well proved to be a problem. All the advanced backcross generations could, however, be produced with relative ease. Environmental conditions in the greenhouse (relative humidity and photointensity) appeared to have a significant effect on the fertility of the hybrid B_nF_1s. High humidity and low photointensity, which were especially prevalent during the winter months influenced the fertility of the hybrid F_1s and, to a lesser extent, the pollen production of the recurrent parent (CS).

4.9. Backcross progenies and their utility

The study has produced the following material: hybrid F_1s with 21 accessions, B_1F_1s with 13 accessions, B_2F_1s with 16 accessions, B_3F_1s with 15 accessions, B_4F_1s with six accessions and B_5F_1s with two accessions (Table 14). The different sources vary in their resistance expression from immune to moderately resistant: (i) Twenty two sources are immune to strongly resistant (IT 0;-;), nine of these are in a fairly advanced stage of backcrossing (B_3F_1 to B_5F_1) (Table 15); (ii) Nineteen hybrids are resistant (IT ;-1$^=$) with six of them having advanced to the B_3F_1; (iii) The rest of the hybrids are resistant (ITs ;-1$^-$ to 1$^+$) or moderately resistant (ITs ;-2$^+$) and mesothetic (IT X). The most advanced generations (B_3F_1, B_4F_1 and B_5F_1) derive from accessions, representative of 10 *Triticum* species, i.e.: *T. turgidum* (AB), *T. timopheevii* (AAGG), *T. speltoides* (SS), *T. sharonense* (SS), *T. kotschii* (UUSS), *T. peregrinum* (UUSS), *T. columnaris* (UUMM), *T. macrochaetum* (UUMM), *T. ovatum* (UUMM) and *T. triaristata* 4*x* (UUMM). The resistance sources used in the most advanced material can than be grouped according to their genomes as follows:

(1) **Genomes group AB and AG:** This includes two *T. turgidum* combinations that have advanced to the B_3F_1. The chromosome numbers of the resistant progeny are $2n = 42$ in both crosses. Fertility is almost normal and a wheat genetic background has obviously been largely restored. Six *T. timopheevii* cross combinations have advanced to the B_5F_1 (3-A-001 with $2n = 42$), B_4F_1 (3-A-005 with $2n = 44$) and B_3F_1 (3-A-014 with $2n = 46$, 3-A-034 with $2n = 41$, 3-A-096 with $2n = 46$ and 4-A-003 with $2n = 46$). Strongly expressed resistance occurs in all instances except the B_5F_1: 3-A-001 which produces a mesothetic infection type.

(2) **Genome group S:** One cross combination involving *T. sharonense* has advanced to the B_4F_1. The resistant progeny shows an immune IT, some degree of fertility and a chromosome number of $2n = 46$. Two cross combinations were produced with *T. speltoides* accessions, and B_5F_1 (3-A-013, IT ;, $2n = 43$) and B_4F_1 (3-A-012, IT ;, $2n =$

44) progeny were derived following their backcrossing to CS. Both derivatives have moderate to good self-fertility.

(3) **Genome group US:** A *T. kotschii* accession has parented one advanced backcross derivative that exhibits strong resistance in the B_3F_1: 3-A-051 (IT ;-1=) and which has a chromosome number of $2n = 43$. However, the selection is self sterile. Three advanced lines were developed following crosses with three *T. peregrinum* accessions. In the three progenies: B_4F_1: 3-A-016 with $2n = 43$, B_3F_1: 3-A-044 with $2n = 42/49$ (mixoploid) and B_3F_1: 3-A-065 with $2n = 43$ the expression of resistance varies from immune (IT 0) to very strong (IT ;). Only B_4F_1: 3-A-016 was self-fertile.

(4) **Genome group (UM):** Three hybrid combinations were derived from *T. columnaris* accessions. All exhibit strong to very strong resistance (IT ; to ;-1=) and are self-fertile. The B_4F_1: 3-A-017 has $2n = 40$, the B_3F_1: 3-A-058 has $2n = 45$ and the B_3F_1: 3-A-066 has $2n = 47/48$ (mixoploid) chromosomes. From *T. macrochaetum* one advanced hybrid combination has been derived (B_4F_1: 3-A-023) which has close to normal fertility, $2n = 41$ chromosomes and produces an IT ;. A cross combination involving a *T. ovatum* accession has advanced to the B_3F_1: 3-A-097. It develops an IT ;-1=, shows good self-fertility and has a chromosome number of $2n = 52$. Finally, from *T. triaristata*, two advanced cross combinations were derived. The B_3F_1: 3-A-100 has excellent resistance (IT 0;, ;) and a chromosome number of $2n = 43$. The B_3F_1: 3-A-107 produces the IT ;-1, has a chromosome number of $2n = 54$, and is partially self-fertile.

All the advanced hybrid progeny phenotypically resemble the wheat parent. The chromosome counts indicate that the genetic background of the wheat parent has largely been restored. The high chromosome number (47-54) retained in some instances, is most probably due to effective chromosome doubling in the colchicine treated F_1 hybrids.

From the chromosome counts it can be deduced that the selection and backcross steps probably resulted in the retention of one or a few alien chromosomes in addition to the wheat chromosomes in many of the backcross derivatives. This will probably be true with regard to donor genomes such as U and M which are more distantly related to the wheat genomes, and it will need to be confirmed with the use of C-banding or *in situ* hybridization procedures. In 42 chromosome individuals the latter techniques may help to distinguish between translocated wheat/alien and substitution chromosomes. In 43 and 44 chromosome individuals it will be necessary to identify the alien chromosome and to develop disomic addition/substitution lines that can be utilized in attempts to transfer the resistance to wheat.

Future attempts to introgress the resistance genes to wheat will largely depend on the level of homology/homeology of the alien donor and wheat chromosomes. From the homologous AB-genomes of *T. turgidum* and the AG-genomes of *T. timopheevii*, gene transfer is expected to occur as a result of homologous recombination. The S-genome (*T. speltoides*, *T. sharonense*, *T. kotschii* and *T. peregrinum*) shares homology and homoeology with the wheat genome and gene transfer may require homologous or homoeologous recombination. Homoeologous exchanges may be enhanced during backcrossing by the presence in some S-genomes of suppressors of *Ph.*

In the more distantly homoeologous transfers involving the M- and U-genomes (*T. kotschii*, *T. peregrinum*, *T. columnaris*, *T. macrochaetum*, *T. ovatum* and *T. triaristata*), the production of addition or substitution lines will be a prerequisite for the incorporation of the resistance genes in wheat chromosomes. It will then be necessary to employ chromosome engineering methodology as described by Sears (1981, 1983). In this material two types of translocation events are possible during backcrossing: (i) those that result from misdivision of univalents during meiosis the so-called Robertsonian translocation and (ii) those resulting from intercalary exchanges of chromatin (non-Robertsonian translocations). If spontaneous translocation do not occur during backcrossing, it will be necessary to achieve homoeologous recombination through the suppression of the *Ph*-system. However, gene transfer from the U- and M-genomes may not always be possible through manipulation of the *Ph* genes. If so, procedures such as ionizing radiation and tissue culture will need to be attempted in order to induce the translocation of alien chromatin onto wheat chromosomes.

Apart from the more advanced material discussed a number of less advanced backcross selections remain. These constitute a very promising source of new genes and further backcrosses with these lines will be continued.

The wild species collection used as the basis of the study is highly diverse (27 *Triticum* and 12 *Thinopyrum* species) and can also serve as starting point for the identification and the transfer of other resistance genes (for example stem rust, mildew, septoria, eyespot disease). In the present study a large number of hybrids was produced and in many cases surplus seeds of the backcross material were obtained and cold stored. These hybrids may be utilized in the search for resistance to other diseases and may simplify future transfer attempts. Also, no attempt was made to identify genes that condition adult plant resistance only. A search for such genes may be undertaken at a later stage.

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6. TABLES

Table 1. Common names and morphological classification of species in the genus *Triticum* (Knott, 1989a).

Species	Common Name	Genome
Einkorn wheats		(2*n* = 2*x* = 14)
T. boeoticum Boiss.	wild einkorn wheat	AA
T. monococcum L.	einkorn wheat	AA
Durum and Emmer wheats		(2*n* = 4*x* = 28)
T. durum Desf.	durum wheat	AABB
T. dicoccum Schrank	emmer wheat	AABB
T. dicoccoides Korn.	wild emmer wheat	AABB
T. turgidum L.	poulard, rivet or corn wheat	AABB
T. polonicum L.	Polish wheat	AABB
T. carthlicum Nevski	Persian wheat	AABB
T. persicum Vav.	Persian wheat	AABB
T. turanicum Jakubz.	No common name	
Timopheevii wheats		(2*n* = 4*x* = 28)
T. timopheevii Zhuk.	No common name	AAGG
T. militinae Zhuk. & Migusch.	No common name	AAGG
Common or Bread wheats		(2*n* = 6*x* = 42)
T. aestivum L.	common or bread wheats	AABBDD
T. compactum Host.	club wheat	AABBDD
T. spelta L.	spelt wheat	AABBDD
T. macha Dek. & Men.	spelt wheat	AABBDD
T. sphaerococcum Perc.	shot wheat	AABBDD
T. vavilovii Jakubz.	No common name	AABBDD
Zhukovski wheat		(2*n* = 6*x* = 42)
T. zhukovskyi Men & Er.	No common name	AAAAGG

Table 2. Taxonomic classifications, genome and plasma type designations of the species of the genera *Triticum* and *Aegilops* according to several workers. The so-called modified genomes are underlined.

Systematic(1	Systematic(2	Genome designation according to: (3	(4	(5	(6-10)	Source of cytoplasm/ plasma type(11
Kingdom:	Plantae					
Division:	Tracheophyta (vascular plants)					
Subdivision:	Pteropsida					
Class:	Angiospermae (flowering plants)					
Subclass:	Monocotyledonae					
Order:	Graminales					
Family:	Gramineae					
Tribe:	Triticeae Dum.					
Subtribe:	Triticinae Holm.					
Genus:	*Triticum* L.					
Section: *Monococca* Flaks.						
T. monococcum L.	*T. monococcum* L.	A				A
ssp. *boeoticum* (Bois.) MK						
ssp. *monococcum*						
T. urartu Thum.						
Section: *Dicoccoidea* Flaks.		A				A
T. turgidum (L.) Thell	*T. turgidum* (L.)					
ssp. *turgidum*		AB		BA		B
ssp. *dicoccoides* (Korn.) Thell		AB				
ssp. *dicoccum* (Schrank) Thell		AB				
ssp. *durum* Desf.		AB				
ssp. *polonicum* L.		AB				
ssp. *persicum* (Percival) Vavilov ex Zhuk.		AB				
T. timopheevii (Zhuk.)	*T. timopheevii* (Zhuk.) Zhuk.	AG		GA		G
ssp. *araraticum* (Jukabz.) MK						
ssp. *timopheevii*						
Section: *Speltoidea* Flaks.						
T. aestivum (L.) Thell						
ssp. *spelta* (L.) Thell		ABD		BAD		B
ssp. *vavilovii* (Tum.) Sears						
ssp. *macha* (Dek at Men.) MK						
ssp. *vulgare* (Vill.) MK						
ssp. *compactum* (Host) MK						
ssp. *sphaerococcum* (Perc.) MK						
T. zhukovskyi Men. & Er.	*T. zhukovskyi* Men. & Er.	AAG			A^mA^uG(6	G
Genus: *Aegilops*						
Section: *Ambylopirum*						
Ae. mutica Boiss.	*T. tripsacoides* (Jaub. & Spach) Bolden	Mt		T	S^m(7	T,T^2
Section: *Sitopsis*						
Ae. sharonensis Eig.				S^l		S^l
Ae. speltoides	*T. speltoides* (Tausch) Gren. ex Richter	S				S,G
var. *speltoides* Tausch						
var. *ligustica* (Savign)Coss.						
Ae. longissima Schweinf. & Muschl. in Muschl.	*T. longissimum* (Schweinf. & Muschl. in Muschl.) Bolden	S^l				S^l

Table 2 continued

Ae. bicornis (Forsk) Jaub.& Sp.	*T. bicorne* Forsk.	S^b				S^b
Ae. searsii Feld. & Kis.	*T. searsii* Feld. & Kis.		S^s			S^s
Section: *Vertebrata*						
Ae. squarrosa L.	*T. tauschii* (Coss.) Schmal.	D				D
Ae. crassa (4x) Boiss.	*T. crassum* (4x) (Boiss.) Aitch. & Hensl.	DJ	DM		$D^cX^{(8}$	D^2
Ae. crassa (6x) Boiss.	*T. crassum* (6x) (Boiss.) Aitch. & Hensl.	DJX	DDM	DDM	$D^cXD^{(8}$	D^2
Ae. vavilovii (Zhuk.) Chenn.	*T. syriacum* Bowden		DMS	DMS	$C^cXS^{s(8}$	D^2
Ae. ventricosa Tausch	*T. ventricosa* Ces.	DM^v	DUn	DN		D
Ae. juvenalis (Thell.) Eig.	*T. juvenale* Thell.		DMU			D^2
Section: *Cylindropyrum*						
Ae. caudata L.	*T. dichasians* (Zhuk.) Bolden	C				C
Ae. cylindrica Host.	*T. cylindricum* Ces.	CD		DC		D
Section: *Comopyrum*						
Ae. comosa Sibth. & Sm.	*T. comosum* (Sibth. & Sm.) Richter	M				M
Ae. uniaristata Vis.	*T. uniaristatum* (Vis.) Richter	M^t	Un	N		N
Section: *Polyeides*						
Ae. umbellulata Zhuk.	*T. umbellulatum* (Zhuk.) Bolden	C^u	U			U
Ae. ovata L.	*T. ovatum* (L.) Raspail	C^uM^o	UM	MU	$UM^{(7}$	M^0
Ae. triaristata (4x) Willd.	*T. triaristatum* (4x) (Willd.) Godr. & Gren.	C^uM^t	UM		$UM^{(9}$	U
Ae. triaristata (6x) Willd.	*T. triaristatum* (6x) (Willd.) Godr. & Gren.	C^uM^tX	UMUn	UMN	$UMX^{(9}$	U
Ae. columnaris Zhuk.	*T. columnare* (Zhuk.) Morris & Sears	C^uM^c	UM			U^2
Ae. biuncialis Vis.	*T. macrochaetum* (Schuttl.& Huet. ex D ıval-Jouve) Richter	C^uM^b	UM			U
Ae. kotschyi Boiss.	*T. kotschyi* (Boiss.) Bowden			SU	$US^{l(10}$	S^l
Ae. variabilis Fig.		C^uS^v	US	SU	$US^{l(10}$	S^s
Ae. triuncialis L.	*T. triunciale* (L.) Raspail					
ssp. *triuncialis*		C^uC	UC			U
ssp. *triuncialis* (Boiss) Zhuk.				CU		C

1 Mac Key (1966)
2 Kimber & Sears (1987)
3 Kihara (in Lilienfeld, 1951)
4 Kimber & Sears (1983)
5 Kimber & Tsunewaki (1988)
6 Mujeeb-Kazi & Wang (1995)
7 Wang (1993)
8 Zhang & Dvorak (1992b)
9 Yen & Kimber (1992)
10 Zhang & Dvorak (1992a)
11 Waines & Barnhart (1992)

Table 3. A synonym list of annual *Triticum/Aegilops* species (Kimber & Feldman 1987b).

Species		Synonyms
Ae. aucheri (aucheri)	=	*T. speltoides*
Ae. bicornis	=	*T. bicorne*
Ae. biuncialis	=	*T. macrochaetum*
Ae. caudata	=	*T. dichasians*
Ae. columnaris	=	*T. columnare*
Ae. comosum	=	*T. comosum*
Ae. crassa	=	*T. crassum*
Ae. cylindrica	=	*T. cylindricum*
Ae. geniculata	=	*T. ovatum*
Ae. heldrechii	=	*T. comosum*
Ae. juvenalis	=	*T. juvenale*
Ae. kotschyi	=	*T. kotschyi*
Ae. ligustica (ligustica)	=	*T. speltoides*
Ae. longissima	=	*T. londissimum*
Ae. longissima v. sharonensis	=	*T. sharonense*
Ae. lorentii	=	*T. machrochaetum*
Ae. markgrafii	=	*T. dichasians*
Ae. mutica	=	*T. tripsacoides*
Ae. neglecta	=	*T. neglecta, T. triaristatum(4x)*
Ae. ovata	=	*T. ovatum*
Ae. peregrina	=	*T. peregrinum*
Ae. persica	=	*T. triunciale*
Ae. recta	=	*T. recta, T. triaristatum(6x)*
Ae. searsii	=	*T. searsii*
Ae. sharonensis	=	*T. sharonense*
Ae. speltoides	=	*T. speltoides (ligustica)*
Ae. squarrosa	=	*T. tauschii*
Ae. triaristata(4x)	=	*T. neglecta*
Ae. triaristata(6x)	=	*T. recta*
Ae. tripsacoides	=	*T. tripsacoides*
Ae. triuncialis	=	*T. triunciale*
Ae. turomanica	=	*T. juvenale*
Ae. umbellulata=		*T. umbellulatum*
Ae. uniaristata	=	*T. uniaristatum*
Ae. variabilis	=	*T. peregrinum*
Ae. vavilovii	=	*T. syriacum*
Ae. ventricosa	=	*T. ventricosum*
T. aegilops	=	*T. tauschii*
T. aegilopoides	=	*T. monococcum*
T. araraticum	=	*T. timopheevii*
T. bicorne	=	*Ae. bicornis*
T. boeoticum	=	*T. monococcum*
T. carthlicum	=	*T. turgidum*
T. columnare	=	*Ae. columnaris*
T. comosum	=	*Ae. comosa, Ae. heldrechii*
T. crassum	=	*Ae. crassa, Ae. vavilovi*
T. cylindricum	=	*Ae. cylindrica*
T. dichasians	=	*Ae. caudata, Ae. markgrafii*
T. dicoccoides	=	*T. turgidum*
T. dicoccum	=	*T. turgidum*
T. durum	=	*T. turgidum*
T. juvenale	=	*Ae. juvenalis, Ae. turomanica*
T. kotschyi	=	*Ae. kotschyi*
T. longissimum	=	*Ae. longissima*
T. mahrochaetum	=	*Ae. biuncialis, Ae. lorentii*
T. monococcum	=	*T. aegilopoides, T. boeoticum, T. urartu*
T. ovatum	=	*Ae. ovata, Ae. geniculata*
T. peregrinum	=	*Ae. peregrina, Ae. variabilis*
T. persicum	=	*T. turgidum*
T. polonicum	=	*T. turgidum*
T. recta	=	*Ae. triaristata(6x)*
T. searsii	=	*Ae. searsii*
T. sharonense	=	*Ae. sharonensis, Ae. londissima v. sharonensis*
T. speltoides (aucheri)	=	*Ae. aucheri*
T. speltoides (ligustica)	=	*Ae. speltoides, Ae. ligustica*
T. syriacum	=	*Ae. vavilovi, Ae. crassa v. vavilovi* or *v. palaestina*
T. tauschi		*Ae. squarrosa*
T. timoph		*T. timopheevii, T. araraticum, T. timopheevii v. zhukovsky*
T. timopheevii v. zhukovsky	=	*T. timopheevii*
T. triaristatum	=	*Ae. triaristata, Ae. recta, Ae. neglecta, T. rectum*
T. tripsacoides	=	*Ae. mutica*
T. triunciale	=	*Ae. triuncialis*
T. turgidum	=	*T. carthlicum, T. dicoccoides, T. dicoccum, T. durum, T. persicum, T. polonicum*
T. umbellulatum	=	*Ae. umbellulata*
T. uniaristatum	=	*Ae. uniaristata*
T. urartu	=	*T. monococcum*
T. ventricosum	=	*Ae. ventricosa*

Table 4. *Triticum* species which occur sympatric (s), sympatric in the northern part of the Fertile Crescent only (n), allopatric (a) or situation unknown (.) (From Kimber & Feldman, 1987b).

		Ploidy levels																													
		[				2n = 2x						]	[					2n = 4x												[1] 2n = 4x]	
		bi	co	di	lo	mo	se	sh	sp	ta	tp	um	un	cl	cy	ko	ma	ne	ov	pe	ti	tr	tu	ve	cr	ju	re	sy			
T. bicorne	(bi)	\	.	.	s	.	.	.	.	.	.	.	.	.	.	s	.	.	.	a	.	.	.	a	.	.	.	.			
T. comossum	(co)	.	\	s	.	a	.	.	s	.	.	s	s	.	a	.	s	s	s	a	.	s	.	.	.	.	.	s	.		
T. dichasians	(di)	.	s	\	.	s	a	.	s	a	s	s	a	s	s	a	s	s	s	a	s	s	s	.	a	a	s	.			
T. longissimum	(lo)	.	a	s	.	\	s	.	s	a	s	a	.	.	.	s	a	.	a	s	.	.	.	.	a	.	.	s			
T. monococcum	(mo)	.	.	a	a	s	\	.	a	.	.	a	.	a	.	a	s	s	s	a	s	s	s	.	a	a	s	.			
T. searsii	(se)	.	.	.	s	.	.	\	a	.	.	a	.	a	.	a	s	a	s	s	s	s	s	.	.	.	.	.			
T. sharonense	(sh)	.	.	.	.	.	.	.	\	.	.	.	.	.	.	.	.	.	a	s	.	.	.	.	.	.	.	.			
T. speltoides	(sp)	.	.	a	s	a	s	a	a	\	a	s	s	.	s	s	.	s	s	s	s	s	s	s	.	a	a	a	.		
T. tauschii	(ta)	.	.	.	a	.	a	.	.	a	\	a	s	.	s	s	a	a	a	a	.	a	s	.	.	s	s	.	.		
T. tripsacoides	(tp)	.	.	.	s	.	s	.	.	s	a	\	s	.	s	s	.	s	s	s	.	a	s	.	.	.	.	.	.		
T. umbellulatum	(um)	.	s	s	.	s	.	.	s	s	s	\	.	s	s	.	s	s	s	.	a	s	.	.	.	.	.	.	.		
T. uniaristatum	(un)	.	.	s	a	.	.	.	.	.	.	.	\	.	a	\	.	a	.	s	s	s	.	.	s	.	.	.	s	.		
T. columnare	(co)	.	.	.	s	.	s	a	.	s	s	s	s	.	\	s	a	s	s	a	a	s	s	.	.	s	s	.	.		
T. cylindricum	(cy)	.	a	s	.	s	.	.	s	s	s	s	a	s	\	a	s	s	s	.	s	s	a	s	s	s	.	a			
T. kotschyi	(ko)	s	.	a	s	.	a	.	.	a	.	a	.	a	a	\	a	.	a	a	.	a	.	.	s	s	.	s			
T. macrochaetum	(ma)	.	s	s	a	s	s	.	s	a	s	s	s	s	s	a	\	s	s	s	s	s	s	a	a	s	.	s			
T. neglecta	(ne)	.	s	s	.	s	a	.	s	a	s	s	s	s	s	.	s	\	s	a	a	s	a	s	a	a	s	.			
T. ovatum	(ov)	.	s	s	a	s	s	a	s	a	a	s	s	s	a	s	a	s	\	s	a	s	s	s	a	a	s	.			
T. peregrinum	(pe)	a	a	s	s	a	s	s	s	.	.	s	.	a	.	a	s	a	s	\	.	s	s	.	.	.	.	a			
T. timopheevii	(ti)	.	.	s	.	s	.	.	s	a	n	s	.	s	s	.	s	a	a	.	\	s	n	.	a	a	.	.			
T. triunciale	(tr)	.	s	s	.	s	s	.	s	s	s	s	s	s	s	a	s	s	s	s	s	\	s	s	s	s	a				
T. turgidum	(tu)	.	.	.	s	.	s	s	.	n	.	.	a	.	a	a	.	s	a	s	s	n	s	\	.	.	.	.			
T. ventricosum	(ve)	a	.	.	.	.	.	.	.	.	.	.	.	.	.	s	a	s	s	s	.	.	s	.	\	.	.	a			
T. crassum	(cr)	.	.	a	a	a	.	.	a	s	.	a	.	s	s	s	a	a	a	.	.	s	.	.	.	\	s	.	a		
T. juvenale	(ju)	.	.	a	.	a	.	.	a	s	.	a	.	s	s	s	a	a	a	.	a	s	.	.	s	.	\	.			
T. recta	(re)	.	s	s	.	s	.	.	a	.	.	s	s	s	.	.	.	s	s	.	.	s	.	a	.	.	.	\			
T. syriacum	(sy)	.	.	.	s	.	.	.	.	.	.	.	.	.	a	s	.	.	.	a	.	a	.	.	a	.	.	\			

1 *T. crassum* contains tetraploid and hehaploid forms

Table 5. Studies that identified resistance/tolerance to biotic and abiotic factors as well as positive variation for agronomically favourable characters in the *Triticum* taxa.

Species	Characteristic and reference
T. bicorne	rust: leaf[16,40], yellow[36]; mildew[16,40]; Hessian fly[16]; BYDV[38].
T. columnare	rust: leaf[16,40], yellow[36]; mildew[16,40]; Hessian fly[16]; BYDV[38], stress[34,47].
T. comosum	rust: leaf[16,50], yellow[1]; mildew[16], Hessian fly[16], bunt[41].
T. crassum	rust: leaf[40]; mildew[16,40], Hessian fly[16], greenbug[16].
T. cylindricum	rust: leaf[16,40,41], yellow[36]; mildew[40], Hessian fly[16], BYDV[38], bunt[41].
T. dichasians	rust: leaf[16,39,40,50], yellow[36,39], stem[39]; mildew[16,39,40], Hessian fly[16], greenbug[16], BYDV[25].
T. juvenale	rust: leaf[40]; mildew[40], bunt[41].
T. kotschyi	rust: leaf[40,41], yellow[36]; mildew[40], drought[1,8,47], heat[1], salt[1], BYDV[38], stress[47].
T. longissimum	rust: leaf[1,16], stem rust[1]; mildew[1,16], Hessian fly[16], greenbug[16], bunt[41], heat[1], drought toler.[1,8], protein content[1].
T. macrochaetum	rust: leaf[16,40,41], yellow[36,47]; mildew[16,40], BYDV[25,38], stress[34,47].
T. monococcum	rust: leaf[23,30,37,41,44], yellow[37,44]; Hessian fly[23], greenbug[30], BYDV[38], protein content[28], photosynthetic capacity[5,33], salt tolerance[32].
T. neglecta/recta	rust: leaf[16,40], yellow[36]; mildew[16,40], Hessian fly[16], BYDV[25,38], bunt[41], stress[47]
T. ovatum	rust: leaf[16,39,40], yellow[36,39,47], stem[39,41]; mildew[16,39,40], Hessian fly[16], stress[34,47], BYDV[38].
T. peregrinum	rust: leaf[16,40,46], yellow[36]; mildew[16,40], Hessian fly[16], greenbug[16], stress[47]
T. searsii	rust: leaf[16], yellow[36].
T. sharonense	rust: leaf[1,16,39], yellow[39], stem[1,39]; mildew[16,39], Hessian fly[16], greenbug[16], salt tolerance[1].
T. speltoides	rust: leaf[1,16,39,46,50], yellow[36,39,45,47], stem rust[1,39]; mildew[16,39], Hessian fly[16], greenbug[16], BYDV[38], photosynthetic capacity[33], bunt[41]
T. syriacum	BYDV[38]
T. tauschii	rust: leaf[4,9,19,23,41,48,49], yellow[49], stem[4,19,48,49]; mildew[9,48], tan spot[48] greenbug[9,23], Hessian fly[9,21,23,26], wheat curl mite[13], salt tolerance[31], photosynthetic capacity[33], stress[47].
T. timopheevii	rust: leaf[1,23,30,43,44], yellow[44], stem[1,43]; mildew[1,29,43], Hessian fly[23,30], protein content[28].
T. triunciale	rust: leaf[16,40,41], yellow[36]; mildew[16,40], Hessian fly[16], stress[34,47], BYDV[25,38], bunt[41].
T. tripsacoides	rust: leaf[40], yellow[36]; mildew[40].
T. turgidum	rust: leaf[1,6,10,14,37,43], yellow[1,6,12,18,20,37], stem[10,15,43]; mildew[6,11,29,43], protein content[1,2,17,18,27,28], photosynthetic capacity[7,33], kernel weight[1,17], earliness[1], drought[22], salt toler.[32], stress[35].
T. umbellulatum	rust: leaf[1,16,40,41,50], yellow[35,45]; mildew[16,40], Hessian fly[16], greenbug[16], BYDV[38], bunt[41].
T. uniaristatum	rust: yellow[45], Al tolerance[1].
T. ventricosum	eyespot resistance[1,3,24], Al tolerance[1], mildew[3], Hessian fly[16]

Characteristics: Resistance to leaf rust, yellow rust, stem rust, powdery mildew, karnal bunt, eyespot, barley yellow dwarf virus (BYDV), Hessian fly, greenbug, wheat curl mite.
Tolerance to frost, heat, drought, stress in general, salt, aluminium (Al).
Improved physiological features such as photosynthetic capacity, grain protein, kernel weight, earliness

References: [1] Kimber & Feldman, 1987; [2] Avivi, 1978; [3] Delibes et al., 1988; [4] Kerber & Dyck, 1978; [5] Austin et al., 1988; [6] Nevo, 1988; [7] Carver & Nevo, 1990; [8] Shimshi et al., 1982; [9] Gill et al., 1986; [10] Bai & Knot, 1994; [11] Moswman et al., 1984; [12] Gerechter-Amitai & Stubbs, 1970; [13] Thomas & Conner, 1986; [14] Moswman et al., 1985; [15] McVey, 1991; [16] Gill et al., 1985; [17] Kushnir & Halloran, 1984; [18] Grama et al., 1983; [19] Kerber, 1994; [20] Grama & Gerechter-Amitai, 1974; [21] Hatchett & Gill, 1983; [22] Blum et al., 1983; [23] et al., 1988; [24] Dosba and Doussinault, 1973; [25] Makkouk et al., 1994; [26] Hatchett & Gill, 1981; [27] Lawren al., 1958; [28] Sharma et al., 1981; [29] Jorgensen & Jensen, 1972; [30] Gill et al., 1983; [31] Gorham et al., 1986; [32] Kashour & Damania, 1991; [33] Austin et al., 1982; [34] Damania & Altunji, 1991; [35] Damania et al., 1991; [36] Van Slageren & Mamluk, 1991; [37] Damania & Skovmand, 1991; [38] Makkouk & Ghoulam, 1991; [39] Valkoun et al., 1985; [40] Frauenstein & Hammer, 1985; [41] Krivchenko et al., 1985; [42] Casulli et al., 1985; [43] Apel', 1984; [44] Dhaliwal et al., 1986; [45] Mikhova, 1988; [46] Manisterski et al., 1988; [47] Damania & Pecetti, 1990; [48] Cox et al., 1992; [49] Appels & Lagudah, 1990; [50] Dhaliwal et al., 1991

Table 6. Wheat relatives grouped according to the genomes they carry and the presumed closeness of their relationships to wheat (adapted from Sears, 1981).

Group	Species	Genome[1]
1. Species having only the A-, B- or D-genomes		
a) the diploid progenitors	*T. monococcum*	A
b) the tetraploid progenitors	*T. tauschii*	D
	T. turgidum	AB
2. Polyploids having one homologous genome		
a) the A-genome	*T. timopheevii*	AG
b) the D-genome	*T. cylindricum*	CD
	T. ventricosum	DN
	T. crassum	D^cX/D^cXD
	T. syriacum	D^cXS^s
	T. juvenale	DMU
3. Species having only homoeologous genomes		
a) closely related species	*T. speltoides*	S
	T. bicorne	S^b
	T. longissimum	S^l
	T. sharonense	S^lI
	T. searsii	S^{sh}
	T. kotschyi	US^l
b) less closely related species	*T. dichasians*	C
	T. comosum	M
	T. tripsacoides	T
	T. uniaristatum	N
	T. umbellulatum	U
	Other U genome polyploids[2]	
	Several *Elitriga* species	
c) distantly related species	Species of *Secale*, *Haynaldia*, *Hordeum*, *Agropyron*, *Elitriga*, etc.	

1 see Table 2.
2 see Fig. 2.

Table 7. The genomes of *Triticum* species and their availability for alien gene transfer (adapted from Kimber, 1993 as cited by Mujeeb-Kazi & Wang 1995).

Genome	Species	Optimum technique, difficulties, availability
A	*T. monococcum*	Recombination[1], partially unreduced gametes possible[2], some genome repatterning[3], good availability[4].
	T. turgidum	Recombination, some genome repatterning, good availability.
	T. timopheevii	Recombination, genome repatterning, available.
	T. aestivum	Recombination from landraces, some genome repatterning, very good availability.
D	*T. tauschii*	Recombination, partially unreduced gametes possible, good availability.
	T. cylindricum	Recombination, meiotic difficulty[5], genome repatterning, available.
	T. ventricosum	
	T. crassum	Recombination, meiotic difficulty, considerable genome repatterning, poor availability.
	T. juvenale	
	T. syriacum	
G[6]	*T. timopheevii*	Recombination, meiotic difficulty, genome repatterning, poor availability.
S[6]	*T. speltoides*	Recombination and/or pairing modifiers active[7] (some S genome accessions contain suppressors
	T. bicorne	of *Ph*), meiotic difficulty, considerable genome repatterning, available.
	T. kotschyi	
	T. longissimum	
	T. searsii	
	T. sharonense	
C	*T. dichasians*	Pairing modification required[8], meiotic difficulty, considerable genome repatterning, poor availability.
	T. cylindricum	Pairing modification required, meiotic difficulty, considerable genome repatterning, poor availability.
M	*T. comosum*	Pairing modification required or ionizing radiation, meiotic difficulty, considerable genome
	T. columnare	repatterning, poor availability.
	T. crassum	
	T. juvenale	
	T. macrochaetum	
	T. ovatum	
	T. syriacum	
	T. triaristatum	
N	*T. uniaristatum*	Pairing modification required or ionizing radiation, meiotic
	T. ventricosum	difficulty, considerable genome repatterning, poor availability.
T	*T. tripsacoides*	Recombination and/or pairing modifiers present (some T-genome accessions contain suppressors of *Ph*), meiotic difficulty,considerable genome repatterning, available.
U	*T. umbellulatum*	Ionizing radiation[9], meiotic difficulty, considerable genome repatterning, poor availability.
	T. kotschyi	
	T. columnare	
	T. juvenale	
	T. macrochaetum	
	T. triaristatum	
	T. triunciale	

1 Homologous recombination with wheat chromosomes is possible.
2 F_1 hybrid with wheat tends to produce restitution nuclei
3 Genome repatterning indicates evolutionary modifications of the genome in the donor.
4 General achievability of a gene transfer
5 Meiotic difficulty indicates possible complications with the introduction of alien variation due to the presence of nonhomologous genomes or translocations.
6 S- and G-genomes are closely related to the B-genome.
7 Contains genes that may modify the expression of the homoeologous pairing control mechanism in wheat.
8 Homoeologous exchange needs to induced through the disruption of the *Ph* mechanism.
9 Introgression may only be achieved through the use of ionizing radiation to induce chromosome breakage and exchange.

Table 8. General procedure for embryo rescue and culturing.

1. Hybridization (early or bud pollination) with optional, prior to and/or post pollination application of hybridizing agents (e.g. 75 ppm aqueous GA3).
2. Embryo excision, as soon as signs of seed deterioration or degeneration is observed, ideally 18-20 days post-pollination.
    a) seed sterilization
    b) aseptic embryo removal
3. Culturing on artificial solid media
4. Incubation under controlled conditions
    a) Temperature regime: 25°- 28° C, with optional, temperature shock for the induction of germination
    b) Lighting: photoperiod continuity (variable, D/L periods)
5. Transplantation and hardening off of plantlets (sterile substrata, sand and/or vermiculite; direct sun protection; increased humidity).

Table 9. Types of wheat aneuploids and their descriptive terms and symbols (Joppa, 1978).

Term	Meiotic configuration	
	Hexaploid	Tetraploid
Nullisomic	20"	13"
Monosomic	20"+1'	13"+1'
Disomic	21"	14"
Trisomic	20"+1'''	13"+1'''
Tetrasomic	$20"+1^{IV}$	$13"+1^{IV}$
Nullisomic-tetrasomic	$19"+1^{IV}$	$12"+1^{IV}$
Monotelosomic	20"+t'	13"+t'
Ditelosomic	20"+t"	13"+t"
Monotelodisomic	20"+1t"	13"+1t"
Double monotelosomic	20"+t'+t'	13"+t"+t"
Double ditelosomic	20"+t"+t"	13"+t"+t"
Dimonotelosomic	20"+t"+t'	13"+t"+t'
Monosomic addition	21"+1'	14"+1'
Disomic addition	21"+1"	14"+1"
Mono-wheat mono-alien substitution*	20"+1'+1'	13"+1'+1'
Di-alien substitution	20"+1"	13"+1"

* Alien substitutions are designated by indicating the chromosome of the alien substitution followed by the wheat chromosome replaced; e.g. 1R(1A) indicates that a pair of 1R chromosomes replaced a pair of 1A chromosomes.

Table 10. Countries that supplied the accessions of the collection.

Country	Number of accessions
Australia	21
Bulgaria	53
Canada	57
France	11
Germany	10
Israel	229
Japan	134
Yugoslavia (Serbia)	12
Russia	24
Sweden	6
Syria	97
Turkey	8
UK	8
USA	232
Unknown origin	54
Total	957

Table 11. The species names of the *Triticum* (classification of Kerber & Feldman, 1987) and *Thinopyrum* (classification of Dewey, 1984) accessions as received and the numbers of accessions per species tested for reaction to leaf rust.

Number of accessions received as:										Total	No tested for leaf rust resistance
species					species						
Triticum					***Aegilops***						
56	(*T. aestivum*)									56	56
3	(*T. bicorne*)				12	(*Ae. bicornis*)				15	15
	(*T. columnaris*)				4	(*Ae. columnaris*)				4	4
2	(*T. comosum*)				1	(*Ae. comosa*)				3	3
	(*T. crassum*)				23	(*Ae. crassa*)				23	23
	(*T. cylindricum*)				15	(*Ae. cylindrica*)				15	15
	(*T. dichasians*)				6	(*Ae. caudata*)				6	6
3	(*T. juvenale*)				1	(*Ae. turomanica*)				4	4
6	(*T. kotschyi*)				1	(*Ae. kotschyi*)				7	7
2	(*T. longissimum*)				16	(*Ae. longissima*)				18	18
	(*T. machrochaetum*)				17	(*Ae. biuncialis*)				17	17
105	(*T. monococcum*)									105	88
	(*T. ovatum*)				17	(*Ae. ovata*)				17	17
	(*T. peregrinum*)				10	(*Ae. variabilis*)				10	10
7	(*T. searsii*)				25	(*Ae. searsii*)				32	32
3	(*T. sharonense*)				10	(*Ae. sharonense*)				13	13
8	(*T. speltoides*)				3	(*Ae. speltoides*)				11	11
	(*T. syriacum*)				34	(*Ae. vavilovi*)				34	34
10	(*T. tauschii*)				20	(*Ae. squarrosa*)				30	30
72	(*T. timopheevii*)									72	72
	(*T. triaristata*)				11	(*Ae. triaristata*)				11	11
2	(*T. triunciale*)				19	(*Ae. triuncialis*)				21	21
344	(*T. turgidum*)									344	344
	(*T. umbellulatum*)				3	(*Ae. umbellulata*)				3	3
	(*T. uniaristatum*)				1	(*Ae. uniaristata*)				1	1
28	(*T. urartu*)									28	17
	(*T. ventricosum*)				5	(*Ae. ventricosa*)				5	5
Thinopyrum					***Agropyron***						
8	*Th. bessarabicum*				1	*A. junceum*				9	9
3	*Th. elongatum*				7	*A. elongatum*, 2*x*				10	10
2	*Th. caespitosum*									2	2
1	*Th. curvifolium*									1	1
3	*Th. distichum*									3	3
7	*Th. junceiforme*									7	7
3	*Th. scirpeum*				3	*A. elongatum*, 4*x*				6	6
5	*Th. intermedium*									5	5
3	*Th. junceum*									3	3
2	*Th. podperae*									2	2
1	*Th. tarcicum*									1	1
2	*Th. ponticum*									2	2
										955	928

Table 12. Avirulence/virulence characteristics of pathotypes of *Puccinia recondita* Rob. ex Desm. f. sp. *tritici* used to study leaf rust resistance in the the wild species collection.

Pathotype	Avirulence/virulence characteristics
UVPrt2	*Lr* 1,2*a*,2*b*,3*ka*,11,15,17,20,24,26,30/2*c*,3*a*,3*bg*,10,14*a*,16
UVPrt3	*Lr* 3*a*,3*bg*,3*ka*,10,11,14*a*,16,17,20,26,30/1,2*a*,2*b*,2*c*,15,24
UVPrt8	*Lr* 3*a*,3*bg*,3*ka*,11,16,20,26,30/1,2*a*,2*b*,2*c*,10,14*a*,15,17,24
UVPrt9	*Lr* 2*a*,2*b*,3*bg*,15,16,17,26/1,2*c*,3*a*,3*ka*,10,11,14*a*,20,24,30
UVPrt13	*Lr* 3*a*,3*bg*,3*ka*,11,16,20,30/1,2*a*,2*b*,2*c*,10,14*a*,15,17,24,26

Table 1.3. Infection type classes produced by 877 *Triticum* (nomenclature after Kimber & Sears, 1987) and *Thinopyrum* (nomenclature according to Dewey, 1984) accessions following their inoculation with an inoculum mix of the pathotypes UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13. The number of successful hybridization attempts and the number of F_1 combinations that expressed the resistance are also indicated.

Species	Genome Designation	Reaction[1] (IT)				No. of acc.	Hybridization results[2]				
		R	MR	MS	S	Total	CR	NV	E	S	NE
T. aestivum	ABD			5	51	56					
T. bicorne	S^b			1	14	15					
T. columnaris	UM	3	1			4	4		3	1	
T. comosum	M			1	2	3					
T. crassum	D^cX/D		2	8	13	23	2				2
T. cylindricum	CD	2	1		12	15	3		2		1
T. dichasians	C	2			4	6	1			1	
T. juvenale	DMU				4	4					
T. kotschyi	US^l	3		2	2	7	3		3		
T. longissimum	S^l	8	2	3	5	18	5	1	1	2	1
T. machrochaetum	UM	10		1	6	17	6		6*		
T. monococcum	A	30	11	9	38	88	6	1		5	
T. ovatum	UM	8	5	3	1	17	10		6	3	1
T. peregrinum	US^l	8		1	1	10	7		7		
T. searsii	S^s	10	2	2	18	32	2	1		1	
T. sharonense	S^s	4		3	6	13	3		2	1	
T. speltoides	S	7	1	3		11	5	1	4		
T. syriacum	C^cXS^s	9	6	14	5	34	4		1		3
T. tauschii	D	2	2	4	22	30	1	1			
T. timopheevii	AG	22	1	11	38	72	23		19	3	1
T. triaristata	UM/X	7			4	11	7		3	3	1
T. triunciale	UC	21				21	21	2	9	8	2
T. turgidum	AB	18	10	39	277	344	28		8	16	4
T. umbellulatum	U	2	1			3	2		2*		
T. uniaristatum	N				1	1					
T. urartu	A		1	2	14	17					
T. ventricosum	DN			1	4	5					
Total		176	46	113	542	877	143	7	76	44	16
Th. bessarabicum	2x	1		2	6	9					
Th. elongatum	2x				10	10					
Th. caespitosum	4x				2	2					
Th. curvifolium	4x	1				1					
Th. distichum	4x			2	1	3					
Th. junceiforme	6x	1		2	4	7					
Th. scirpeum	4x				6	6					
Th. intermedium	6x	2			3	5					
Th. junceum	6x	2			1	3					
Th. podperae	6x				2	2					
Th. turcicum	8x	1				1					
Th. ponticum	8x	1		1		1					
Total		9		7	35	51					

[1] Reactions: R - resistant, MR - moderately resistant, MS - moderately susceptible, S - susceptible.

[2] Hybridisation results: CR - the number of crosses that produced seeds, NV - the number of crosses that produced inviable seeds, E - number of crosses in which complete resistance was expressed in the F_1, S - number of crosses in which resistance was not expressed in the F_1, NE - number of crosses in which the resistance was not effective against all the pathotypes used.

* F_1 plants from one cross were produced and were resistant, but later died.

Table 14. A summary of backcross results obtained with the most promising sources of resistance.

Cross	F_1 infection type (IT)		F_1 self fertility	Most advanced backcross:		
	pathotype mix[1]	UVPrt8		Generation	IT with UVPrt8	Chromosome number ($2n$)
CS x *T. columnaris*						
3-A-017 (CS/588-COL)	;1	;1	No	B_4F_1 (B_4F_2)	;	40
3-A-058 (CS/614-COL)	;-1=		Yes	B_3F_1 (B_3F_2)	;-1=, X, ;1=-3	45
3-A-066 (CS/128-COL)	;-2	X	Yes	B_3F_1 (F_2)	;, 2=	41-48
CS x *T. cylindricum*						
4-A-064 (CS/183-CY)		;-1+	No	F_1	-	
3-A-059 (CS/590-CY)	1-2		Yes	B_2F_1 (B_1F_2)	;-1=, ;2+	
CS x *T. kotschyi*						
3-A-051 (CS/676-KO)	;1=		Yes	B_3F_1 (B_3F_2)	;-1=	44
4-A-032 (CS/678-KO)		;1C	No	B_1F_1	;, ;-1 ,;-2=	
4-A-096 (CS/617-KO)		0;	No	F_1	-	
T. longissimum/*T. monococcum*//CS						
4-A-115 (483-LO/972-MO//CS)	;C-4Z		No	F_1	-	
CS x *T. mocrochaetum*						
3-A-023 (CS/683-MA)	;1=		No	B_4F_1 (B_4F_2)	;, ;-1=, X	47
4-A-162 (CS/762-MA)		;	No	F_1	-	
4-A-150 (CS/763-MA)		;-1=Z	No	F_1	-	
4-A-151 (CS/766-MA)		;-1=	No	F_1	-	
4-A-159 (CS/768-MA)		;N-1=Z	No	F_1	-	
CS x *T. ovatum*						
3-A-097 (CS/757-OV)	2+	;-2-C	Yes	B_3F_1 (B_2F_2)	;-1=, X	52
4-A-063 (CS/146-OV)		;-2Z	No	F_1	-	
4-A-112 (CS/693-OV)		;-2=Z	No	F_1	-	
4-A-138 (CS/755-OV)		;-1=, ;-1Z	No	F_1	-	
4-A-139 (CS/758-OV)		;-2+Z	No	F_1	-	
4-A-143 (CS/760-OV)		;-1+	No	F_1	-	
CS x *T. peregrinum*						
3-A-016 (CS/673-PE)	;-1=	;1-	No	B_4F_1 (B_4F_2)	;, X	43
3-A-044 (CS/488-PE)	;N		Yes	B_3F_1 (B_3F_2)	0;	42-49
3-A-065 (CS/161-PE)	;1-		No	B_3F_1 (B_3F_2)	;, X	44
4-A-021 (CS/702-PE)		;-1=	Yes	B_1F_1 (F_2)	;, ;1-	
4-A-023 (CS/682-PE)		;1N	No	B_1F_1	;-1=, ;-1+Z	
4-A-087 (CS/680-PE)		;-1=	No	F_1	-	
4-A-090 (CS/909-PE)		;-1C	Yes	B_1F_1 (F_2)	;, ;-1=, ;2+	
CS x *T. sharonense*						
3-A-010 (CS/174-SH)	;-1=		No	B_4F_1 (B_4F_2)	0;, ;-1=, ;-1-	46
4-A-025 (CS/148-SH)		;1=	Yes	B_2F_1 (B_1F_2)	;-2Z	
CS x *T. speltoides*						
3-A-012 (CS/681-SP)	;1=	;-1=	Yes	B_4F_1 (B_4F_2)	0;, ;, X	44
3-A-013 (CS/691-SP)	;	;1=	Yes	B_5F_1 (B_5F_2)	;, ;-1=, ;1=, X	43
4-A-137 (CS/692-SP)		0;	No	F_1	-	
CS x *T. syriacum*						
4-A-022 (CS/849-SY)		;-1=	No	B_1F_1	;, ;-1+Z, ;-2+Z	

Table 14 ...ntinued

CS x T. timopheevii						
3-A-001 (CS/260-TI)	;1=-1	;-1	Yes	B_5F_1 (B_5F_2)	X	42
3-A-002 (CS/201-TI)	;1	;-1-	Yes	B_2F_1 (F_2)	;-1=	
3-A-003 (CS/185-TI)	;1-	X	Yes	B_2F_1 (B_1F_2)	;1=C-3C	
3-A-005 (CS/479-TI)	0;N	;, ;-1=	No	B_4F_1 (B_4F_2)	0;, ;	44
3-A-014 (CS/648-TI)	;-1=	;-1	Yes	B_3F_1 (B_2F_2)	;, ;-1=, X	46
3-A-022 (CS/653-TI)	;1=	;-1	Yes	B_3F_1 (B_2F_2)	4	
3-A-029 (CS/255-TI)	;1=	;1=, ;1-	Yes	B_2F_1 (B_1F_2)	;-1-, ;1-	
3-A-030 (CS/654-TI)	;1-3	;1++, ;2-	Yes	B_2F_1 (B_1F_2)	;-1=	
3-A-031 (CS/253-TI)	4	;-1-	No	B_2F_1	;	
3-A-032 (CS/254-TI)	4	;1+	No	B_2F_1	;-1=	
3-A-033 (CS/639-TI)	;1=	;1=	No	B_1F_1	4	
3-A-034 (CS/200-TI)	;N	;-1=	No	B_3F_1 (B_3F_2)	;-1=, ;1=, ;-1	41
3-A-054 (CS/256-TI)	;1-	;1-2	Yes	B_1F_1 (F_2)	;, ;-1, ;1=-2Z	
3-A-096 (CS/258-TI)	;-1=	;-2Z	Yes	B_3F_1 (B_3F_2)	;-1=, X	51/46
3-A-118 (CS/ 76-TI)	;-1-	X	Yes	B_2F_1 (B_1F_2)	;-2+	
4-A-002 (CS/199-TI)		;-1+	Yes	B_2F_1 (B_1F_2)	;-2	
4-A-003 (CS/259-TI)		;-1-	Yes	B_3F_1 (B_3F_2)	;-1=, X	46
4-A-009 (CS/256-TI)		;	Yes	B_1F_1 (F_2)	;	
4-A-065 (CS/257-TI)		X	No	B_1F_1	3+,4	
CS x T. triaristata						
3-A-100 (CS/155-TRT)		0;	No	B_3F_1	0;, ;	43
3-A-107 (CS/750-TRT)	;1+	1-	No	B_3F_1 (B_2F_2)	;-1, X	54
3-A-119 (CS/749-TRT)	2		Yes	B_1F_1 (F_2)	;-1=, ;-1-, ;-1	
CS x T. triunciale						
3-A-069 (CS/157-TR)	;	;	No	B_2F_1	;N, ;-1C	
4-A-054 (CS/156-TR)		;N-1-	No	F_1	-	
4-A-095 (CS/779-TR)		;2	No	F_1	-	
4-A-129 (CS/773-TR)		;-2Z	No	F_1	-	
4-A-130 (CS/7811-TR)		;-1=	No	F_1	-	
4-A-131 (CS/7812-TR)		;-1=	No	F_1	-	
4-A-145 (CS/838-TR)		;-1=	No	F_1	-	
CS x T. turgidum						
3-A-021 (CS/525-TUDS)	1		Yes	B_1F_1 (B_1F_2)	X	
3-A-045 (CS/2611-TUDI)	;1-2		Yes	B_3F_1 (B_3F_2)	;, X	42
3-A-049 (CS/2612-TUDI)	;-3	;, ;1=	Yes	B_2F_1 (B_1F_2)	;, ;N-1-, ;N	
3-A-057 (CS/659-TUDU)	;1		Yes	B_3F_1 (B_3F_2)	;-1=, ;-1, X	42
3-A-062 (CS/283-TUDU)	;-2=		Yes	B_2F_1 (B_1F_2)	;, ;-1=, X	
3-A-092 (CS/365-TUDS)		;	Yes	B_1F_1 (F_2)	;, ;-1=N	
4-A-004 (CS/325-TUDS)		;-1+	Yes	B_2F_1 (B_1F_2)	;, ;-1=	
4-A-008 (CS/645-TUTU)		;-2=Z	Yes	B_2F_1 (B_1F_2)	X	
CS x T. umbellulatum						
3-A-104 (CS/740-UM)	;	;	Yes	B_2F_1 (F_2)	;-1=	

[1] Pathotypes UVPrt2, UVPrt3, UVPrt8, UVPrt9 and UVPrt13.

Table 15. Leaf rust resistant *Triticum* accessions which also produced resistant F_1 hybrids in crosses with wheat.

Accession	Source	IT with a mix of 5 pathotypes[1]	IT with leaf rust pathotype: UVPrt2	UVPrt3	UVPrt8	UVPrt9	UVPrti3
T. columnaris							
128-COL	USA	1+	;-1=	;	;N	;	;1=
588-COL	CAN	;	0;	;-1=C	;	;	;
614-COL	ISR	;1=	;1=C	;C-1=	;,;1=C	0;	;-1=
T. cylindrycum							
183-CY	AUS	;-2,;1=,;N	;	;	;	;N-1=	;C
590-CY	CAN	;	;N	;	;	;-1=	;
T. kotschyi							
617-KO	ISR	;	;N	0;	0;	;	;
676-KO	ISR	;1-	;1=C	;1=C	;1-C	;-1=	;C
678-KO	ISR	;-2=,;1	2=C	;-1=C	;-1-C	;-1	
T. longissimum							
483-LO	ISR	;1-	;	;	;1=	;	
T. macrochaetum							
683-MAC	ISR	;1=	;1-	;-1=C	;1	;-1-	-
762-MAC	BG	0	0	0	0,	0	0;
763-MAC	BG	0	0;	;	;	0;	;
766-MAC	BG	0;	0;	0;	0;	0	;
768-MAC	BG	0;	0	0	0	0;	0
T. ovatum							
146-OV	USA	2	2C	;	;-1-	;2	-
693-OV	ISR	;	;N	;-1=C	;	;	;
755-OV	BG	;1-	X	;-1=	-1C	;-2	-
757-OV	BG	;1=N	;C-1=	;N	;N	0;	-
758-OV	BG	;1-	;N-1=	;C	0;	;C	;1+C
760-OV	BG	;-1++,;1=	0;	;	1	;	-
T. peregrinum							
161-PE	USA	;-1-	;-1-	;N	;-2=	;-1=	-
488-PE	USA	;1-	;N	0;	;	0;	;C
673-PE	USA	;-1=	;-1=N,;N	;	;-1=	;	-
680-PE	ISR	;1-	;N	0	;	;-1=	-
682-PE	ISR	;-1	;N	;C	;C	;N	
702-PE	ISR	2=	;-1=N	0;	;	0;	-
909-PE	Unknown	;1	;	;	;N	;-1=	;1=
T. shoronense							
148-SH	USA	;-1+,;1=	2=	;1-	X	X	;-1=
174-SH	ISR	;	;	;	;	0;	;
T. speltoides							
681-SP	ISR	;	;N	;	;N	;	;
691-SP	ISR	;1-	;	;C	;	;-1=	-
692-SP	ISR	;	0;	0;	0	0;	0;

Table 15 continued

T. syriacum							
849-SY	SYR	X,;	0;	;	0;	0;	;
T. timopheevii							
185-TI	Unknown	;,;1	;	;	;	;	;
199-TI	GER	;1-	;N	;C	;	;	;C
200-TI	GER	;-1	;	;	;	;C	;C
201-TI	GER	;1-	0;	;C	;	;C	-
253-TI	JAP	;	;CN-1=	;N	;	;	-
254-TI	JAP	;	;CN	;	0;	;	;
255-TI	JAP	;	;N	;	0;	;	-
256-TI	JAP	;	;	;	0;	;N	-
257-TI	JAP	;-1=,;	;N	;C	;	;	-
258-TI	JAP	0;	0;	;N	;	;N	0;
259-TI	JAP	;	0;	.	0;	;	;
260-TI	JAP	;	0;	;N	;	;	-
479-TI	Unknown	;	;1=	;-1=C	;	0;	;1=
639-TI	ISR	;-;1=	;CN	;N	;	;	;1=
640-TI	RUS	0;	;CN	;C	2=C	;	;-1=
648-TI	Unknown	;-1=	0;	;	;C	;	-
653-TI	USA	;	;N	;CN	;C	;C	;N
654-TI	USA	;	;N	0;	;	;N	;C
076-TIA	USA	;1+,3=	;-1=	;-1+	;	X	-
T. triaristata							
155-TRT	USA	;1-	;1-	;	;-1-	1=	-
749-TRT	BG	;1-	;-1-N	;C	0;	;C	;-1-
750-TRT	BG	;-1=N	;N	;CN	;N	;N	-
T. triunciale							
156-TR	USA	;-1=,;1=	;N	0;	;N	0;	-
157-TR	USA	;1=	;-1-	;-1=C	0;	;1=	-
773-TR	BG	;1-	2=C	;	;-1+C	0;	1-
777-TR	BG	0;	;1C	;	0	;	-
778-TR	BG	;-1=	0;	;1C	;1=	;	-
779-TR	BG	;-1	;1-	;	0;	;	;-1=C
781-TR	BG	;1-	;N	;	;	0	-
7812-TR	BG	;2-	;1=	;	;C,;	;	-
838-TR	Unknown	;1=	;,;-1=	;C	;CN-1=	0;	-
T. turgidum							
2611-TUDI	JAP	;2-	;2=C	2-	;	;N	;C
2612-TUDI	JAP	;	;	;N	;	0;	;
325-TUDS	ISR	;1,X	;-2=C	;-1=C	;-1=	;1=	-
365-TUDS	ISR	;	;1	;C	;	;C	;
525-TUDS	Unknown	;1,X	0;	;-2+Z	X	;1+	-
283-TUDU	JAP	;2,;1	;C-i=	;	;1	1+	-
659-TUDU	Unknown	;1=	;N	;-1=	;CN	;-1=	-
645-TUTU	RUS	;,;N	;N	;N	0;	;N	;
T. umbellulatum							
740-UM	BG	0;	;CN	;N	0;	;N	;

[1] Pathotypes: UVPrt2, UVPrt3, UVPrt8, UVPrt9, UVPrt13

7. FIGURES

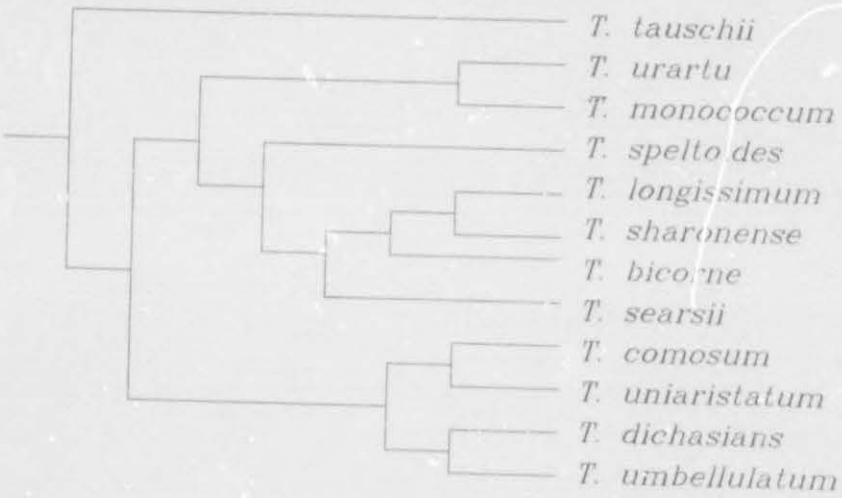


Fig. 1. Phylogenetic tree of the diploid *Triticum* species based on variation in the restriction fragment length patterns of repeated nucleotide sequences (Dvorák & Zhang, 1992).

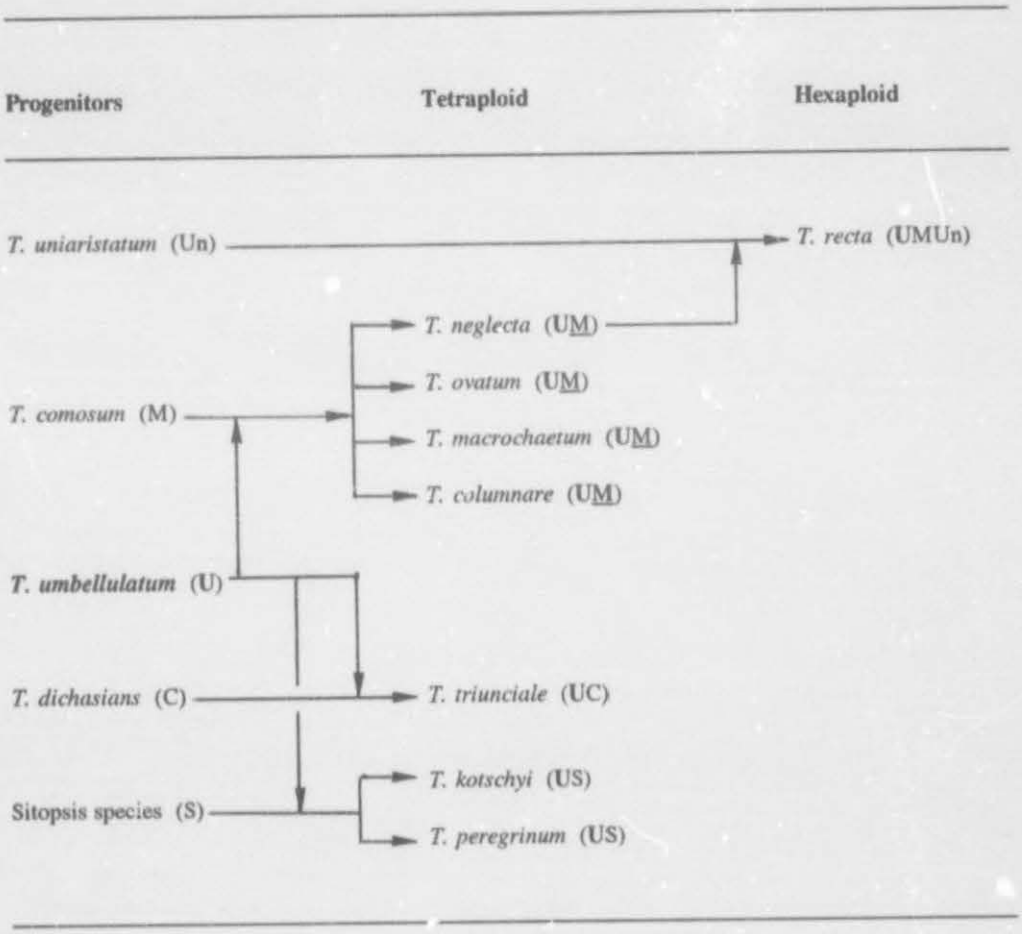


Fig. 2. A diagrammatic representation of the major evolutionary features of the U-genome carrying wild wheat species (Kimber & Feldman, 1987a).

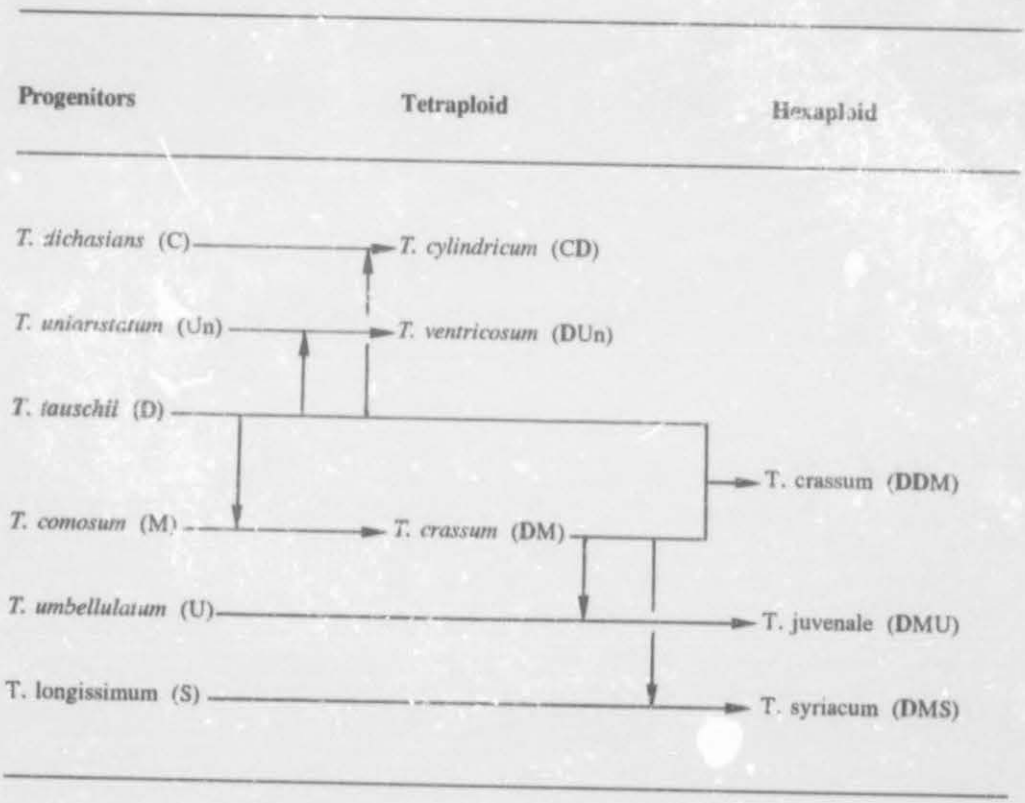
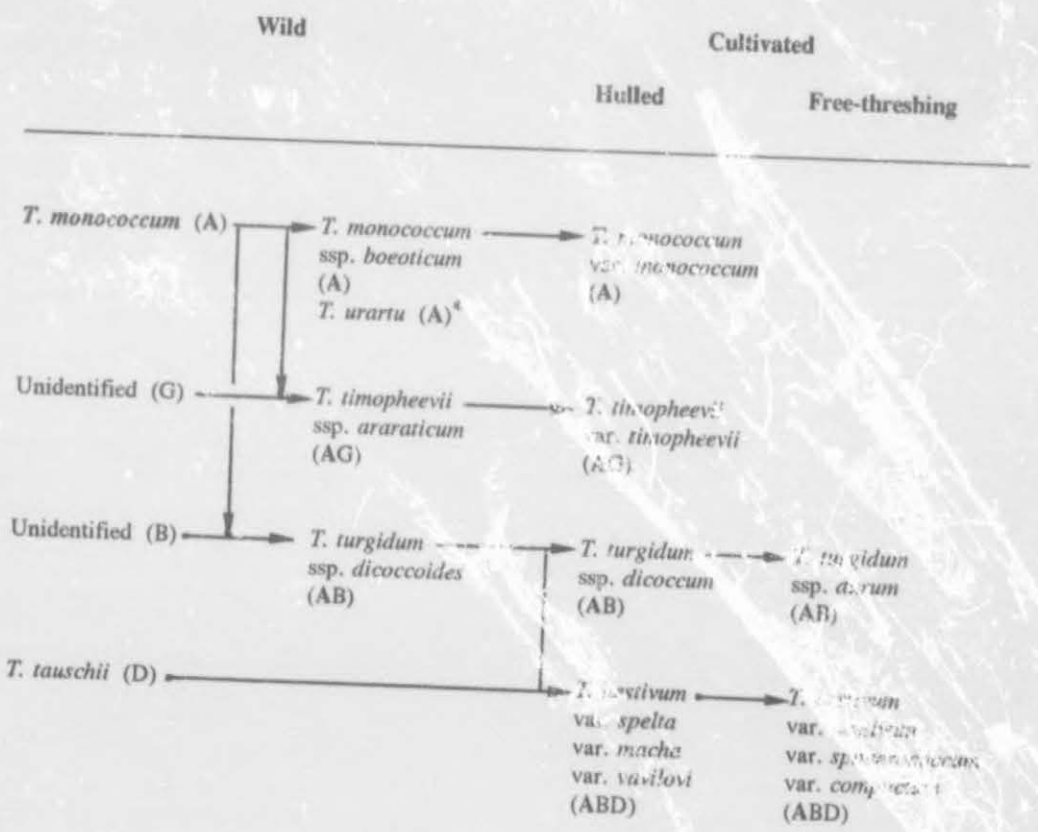


Fig. 3. A diagrammatic representation of the major evolutionary features of the D-genome carrying wild wheat species. Evolution in this cluster was characterized by two major events. The first left the tetraploids, *T. cylindricum* and *T. ventricosum* (Yen & Kimber, 1992) with essentially unaltered D-genomes. The second involved tetraploid *T. crassum* species and resulted in the formation of hexaploids with substantially modified D-genomes (Kimber & Feldman, 1987a).



* At present *T. uraru* is regarded as a separate species (Morrison, 1993).

Fig. 4. A diagrammatic representation of the major evolutionary features of the A-genome carrying wild and cultivated wheat species. For simplicity possible introgression between the tetraploid species is not shown (Kimber & Feldman, 1987a).

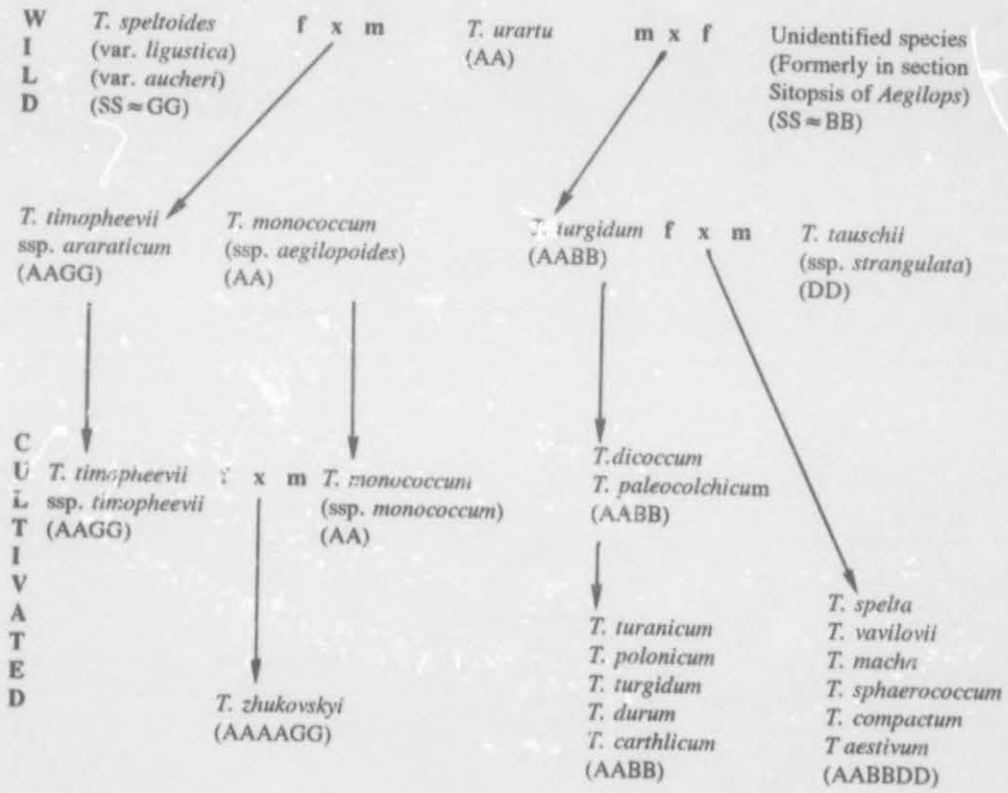


Fig. 5. Evolutionary origin of cultivated wheat (AABBDD and AAAAGG) (Dvorák, 1993; Miller, 1987; Kimber & Feldman, 1987; Kimber & Sears, 1987; Juang & Gill, 1994; Shands & Kimber, 1973; Tsunewaki & Ogihara, 1983; Dvorák et al., 1989; Miyashita et al., 1994; Knott, 1989a; Juang & Gill, 1994).

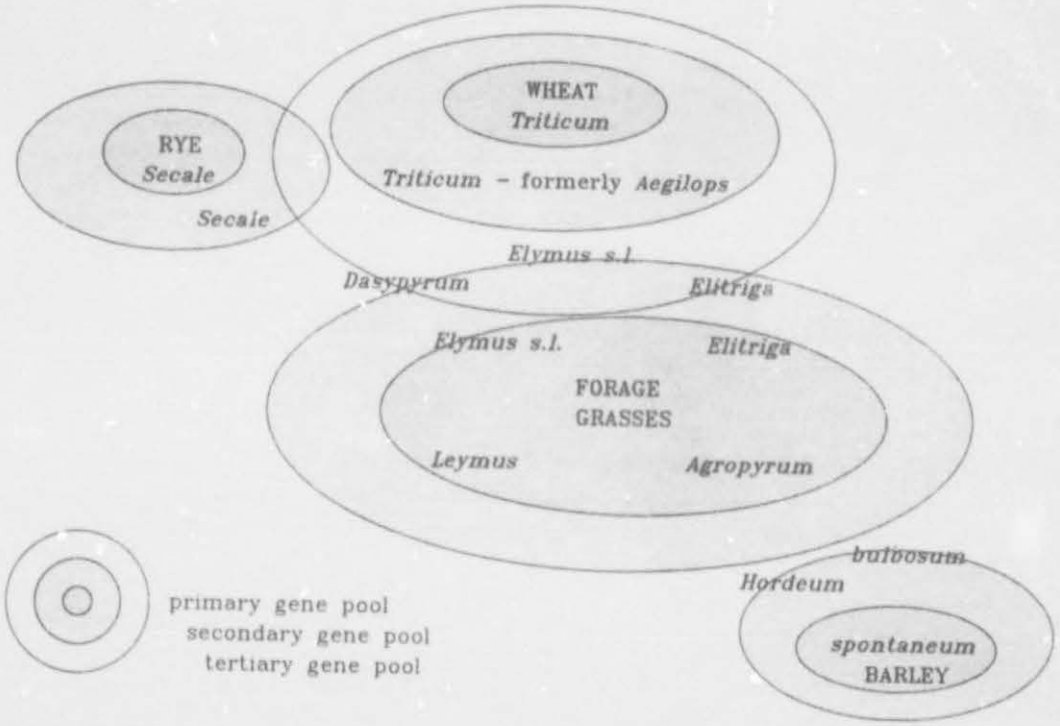
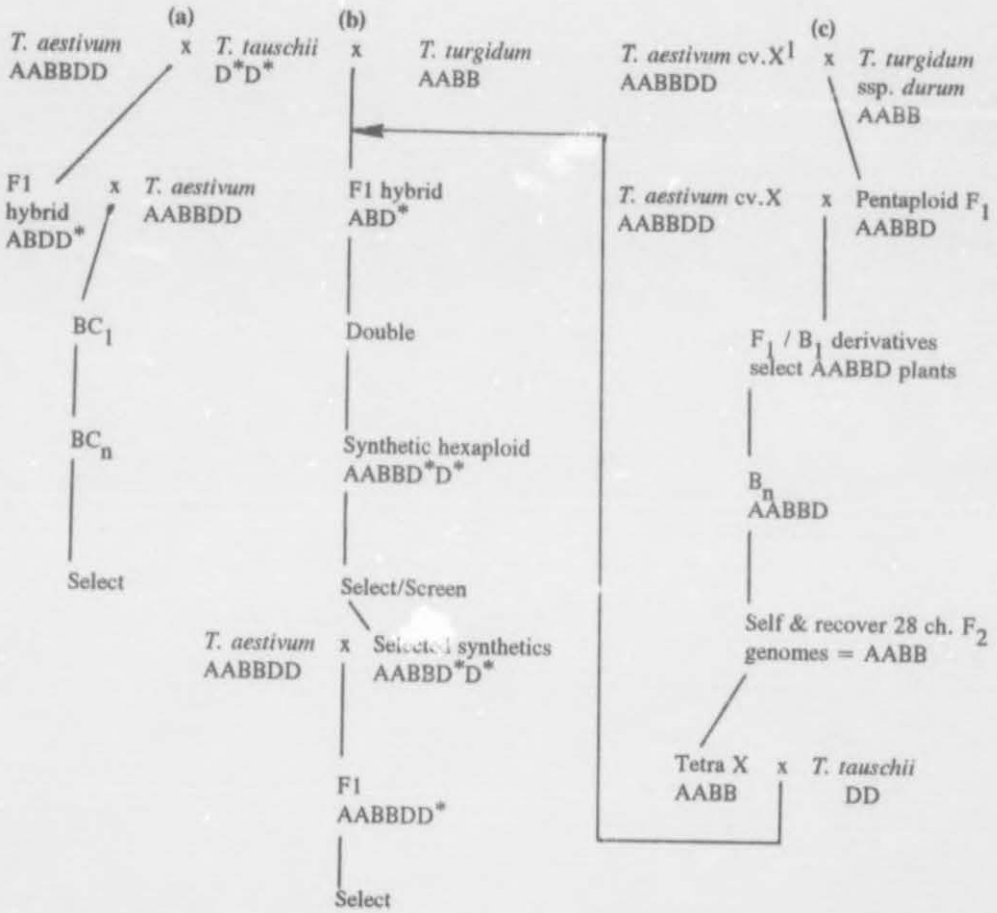


Fig. 6. Gene pools in the Triticeae (Bothmer et al. 1992).

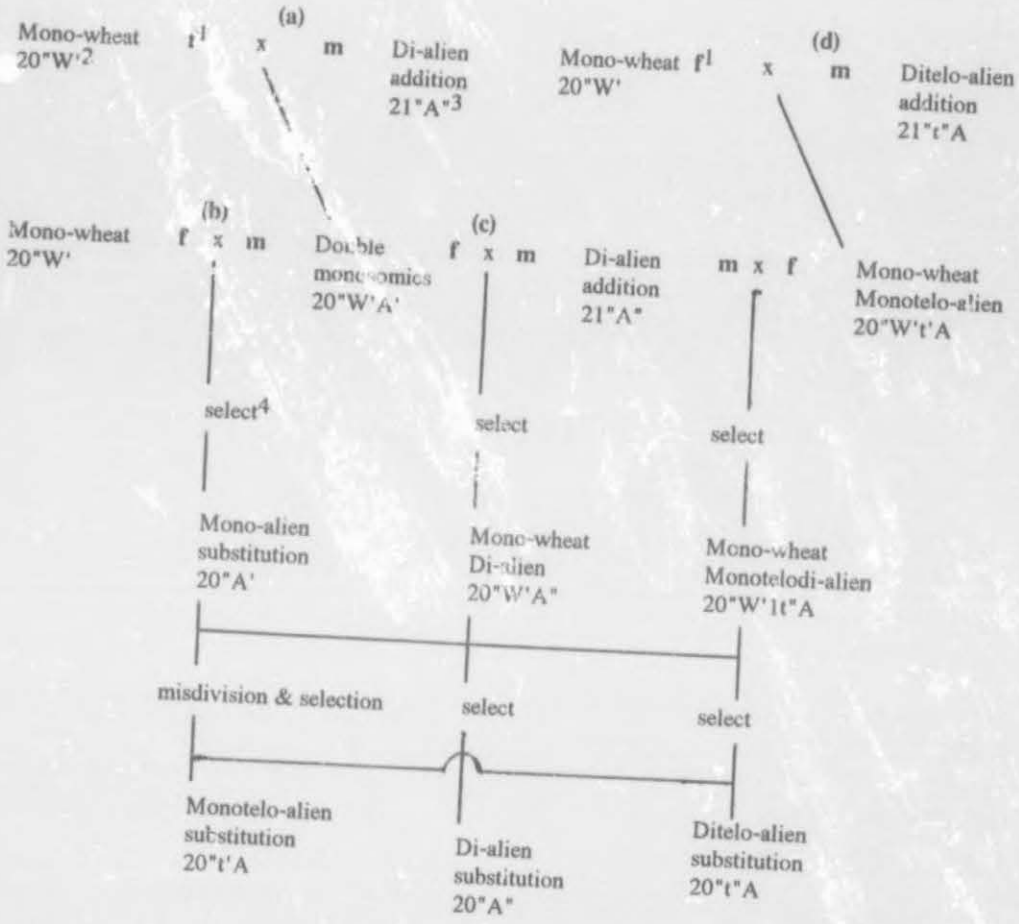


1 cv. X - any hexaploid wheat cultivar

Fig. 7. Gene transfer from *T. tauschii* to *T. aestivum* via (a) direct crossing and backcrossing (BC), (b) the use of a tetraploid bridging species or (c) the use of an extracted tetraploid bridge genotype.

1 sex of the parents is noted only when the direction of the cross is critical.
2 alien genome/chromosome
3 chromosome doubling
4 selection for chromosome number

Fig. 8. Cytogenetic methods for the production of wheat-alien addition lines. (a) Knott, 1987, 1989b; (b) Sears, 1981, Knott, 1987, 1989b; (c) Gale & Miller, 1987, Barcley, 1975; (d) Laurie & Bennett, 1986.



1 sex of the parents is noted only when the direction of the cross is critical.
2 wheat chromosome
3 alien chromosome
4 selection for chromosome number

Fig. 9. Cytogenetic methods for the production of an alien substitution line. (a) Sears, 1981, Feldman & Sears, 1981; (b) and (c) Knott, 1987, 1989b; (d) Gale & Miller, 1987.

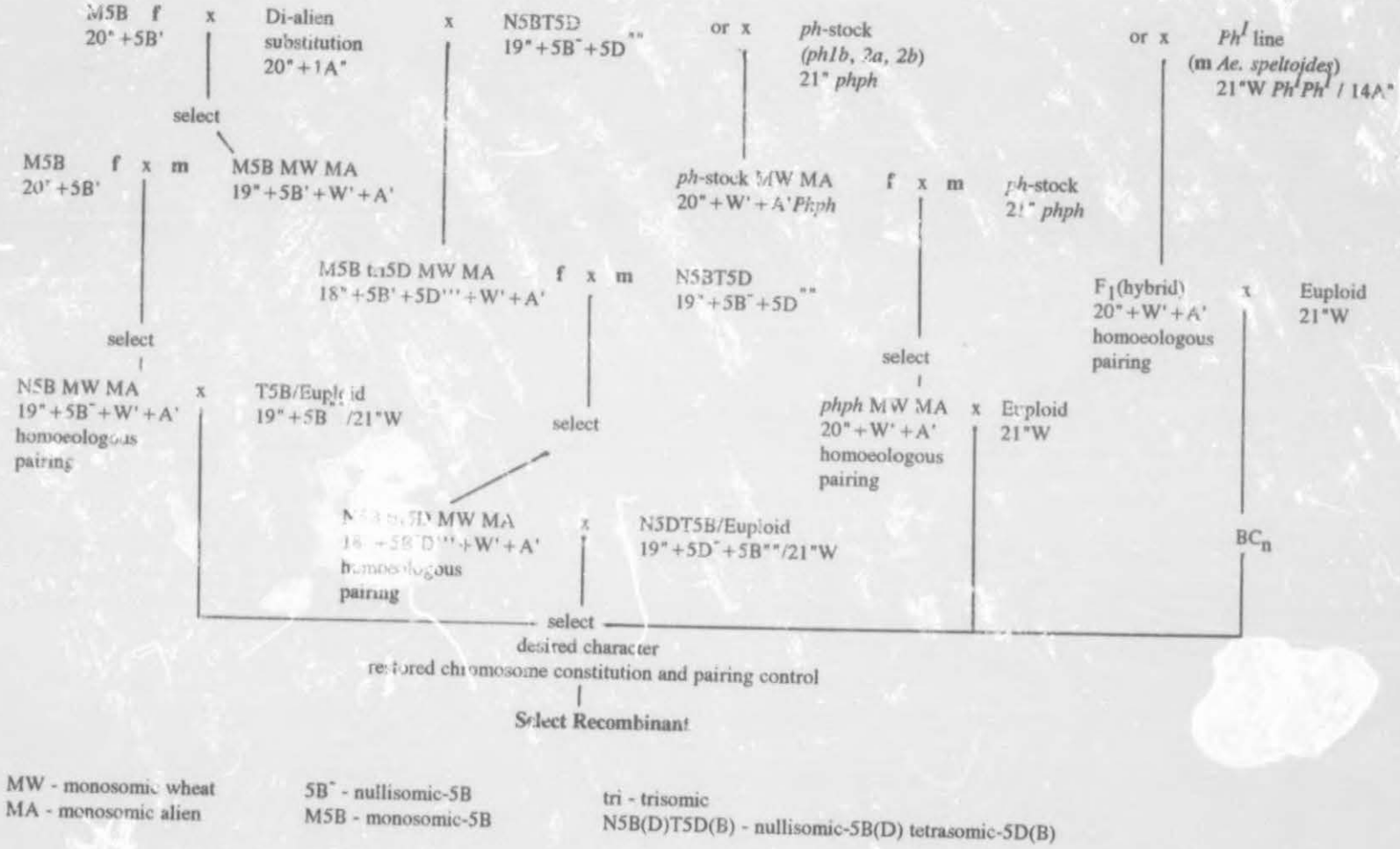


Fig. 10. Methods for the production of *ph*-induced wheat-alien translocations (Knott & Dvorák, 1976 Sears, 1981, 1984; Feldman & Sears, 1981; Gale & Miller, 1987; Feldman 1988; Gustafson & Dera 1989)

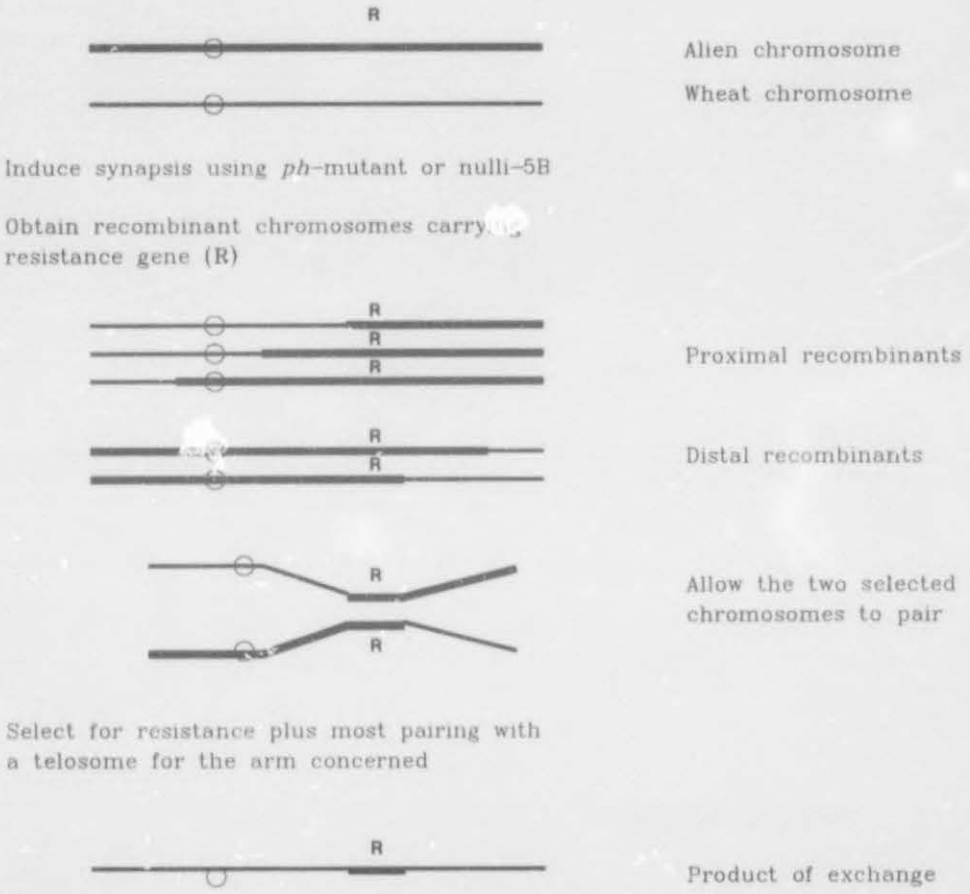


Fig. 11. Procedure for the shortening of a transferred alien segment by allowing recombination between two selected translocation chromosomes (Sears, 1972, 1981, 1983).

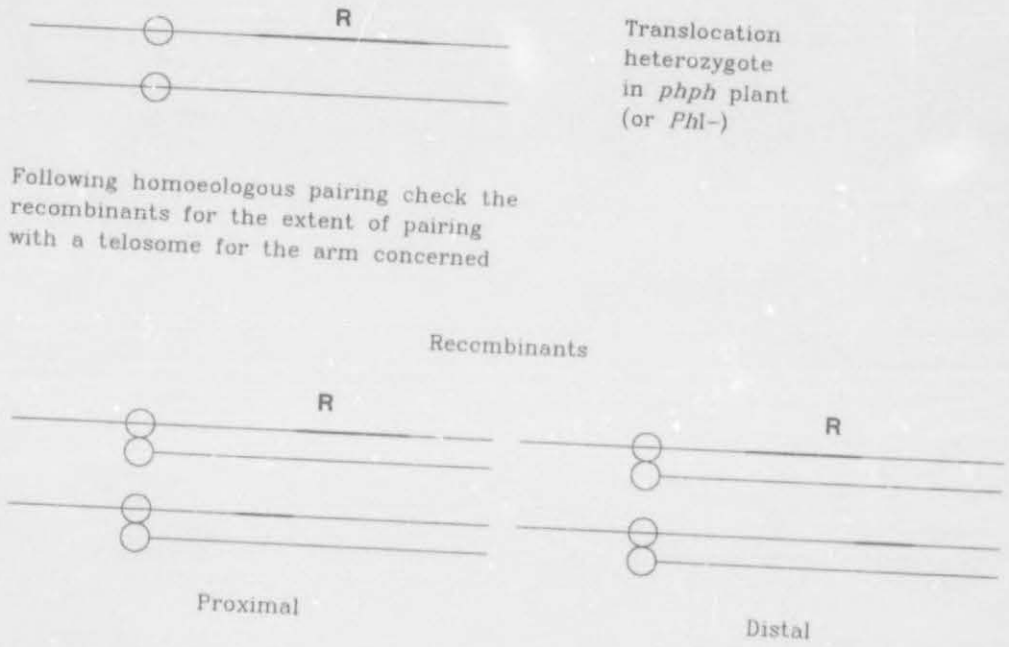


Fig. 12. Shortening of an interstitial alien segment by inducing it to pair with the corresponding portion of its wheat homoeologue (Sears, 1983).